

**MAMMAL – PLANT DYNAMICS IN FORESTS: INTERACTIONS AND  
IMPLICATIONS FOR UNDERSTORY PLANT DIVERSITY**

by

Alejandro A. Royo De Sedas

B.A. in Biology, University of North Carolina, Greensboro, 1993

M.S. in Biology, University of North Carolina, Greensboro, 1998

Submitted to the Graduate Faculty of

Arts and Sciences in partial fulfillment

of the requirements for the degree of

Ph.D. in Ecology

University of Pittsburgh

2005

UNIVERSITY OF PITTSBURGH  
FACULTY OF ARTS AND SCIENCES

This dissertation was presented

by

Alejandro A. Royo De Sedas

It was defended on

June 27, 2005

and approved by

Stephen B. Horsley, Ph.D.

Joseph Merritt, Ph.D.

Rick Relyea, Ph.D.

Steve Tonsor, Ph.D.

Walter P. Carson, Ph.D.  
Dissertation Director

# **MAMMAL – PLANT DYNAMICS IN FORESTS: INTERACTIONS AND IMPLICATIONS FOR UNDERSTORY PLANT DIVERSITY**

Alejandro A. Royo De Sedas, PhD

University of Pittsburgh, 2005

In forest communities, the composition and abundance of plants in the understory is generally mediated via a complex interplay between herbivory and competition. Nonetheless, most research assesses the effect of herbivory and competition independently and rarely investigates potential interactions between the two factors. In this dissertation, I examine how herbivory and competition, alone and in concert, influence forest understory plant diversity. At one extreme, herbivory is hypothesized to reduce interspecific competition, thus allowing for greater species coexistence in the understory. In chapter one, I test this hypothesis in the herbaceous community of a tropical forest in central Panamá. I found mammals limited the abundance of the dominant herbs while simultaneously limiting the establishment of rare species. In contrast, intense herbivory may reduce the diversity of the most palatable species allowing browse-resistant species to rapidly expand and overtake the forest understory. In chapter two, I explore this alternative by reviewing the processes leading to the formation of recalcitrant understory layers worldwide and summarizing the mechanisms by which these layers inhibit tree seedling regeneration and alter forest succession. In chapter three, I experimentally examine how a recalcitrant understory layer limits tree species recruitment via direct competitive as well as indirect, apparent competitive interactions. Specifically, by providing a favorable microhabitat for small mammals, a dense understory canopy can facilitate increased granivory, thereby indirectly limiting tree recruitment. I found a dense hay-scented fern (*Dennstaedtia*

*punctilobula*) understory exerts strong apparent competitive effects on the emergence of black cherry (*Prunus serotina*) and strong competitive effects on emergence and survival of red maple (*Acer rubrum*). In chapter four, I explore the potential interactions between white-tailed deer (*Odocoileus virginianus*) and a dense canopy of hay-scented fern. This work demonstrates that in light limited, closed-canopy forests, a dense understory layer strongly suppresses germination and survival of several shade intolerant tree species. Furthermore, I argue that century-long legacy of deer overbrowsing has resulted in a depauperate forest community that predisposes future declines in plant diversity and increased monodominance. In all, these findings stress the need to discriminate among multiple ecological factors and assess their relative importance in structuring natural communities.

## **ACKNOWLEDGEMENTS**

I owe thanks to many people for their professional and personal support during the fulfillment of this dissertation. First, I thank my advisor, Walter Carson for rigorously guiding my professional development. Throughout my tenure at the University of Pittsburgh, Walt has become both a close collaborator and a personal friend. I also thank Steve Horsley for innumerable debates and patient instruction on various aspects of forest ecology. I also am deeply indebted to Joe Merritt, Rick Relyea, and Steve Tonsor for their advice, comments, and critiques throughout the various stages of this dissertation. I have benefited greatly from all the Ecology and Evolution graduate students with whom I have overlapped, in particular, Stefan Schnitzer, Dan Bunker, Rachel Collins, James Cronin, Tony Baumert, and Henry Schumacher. Our countless conversations regarding science and life have contributed to my growth as an ecologist and an individual. I am personally indebted to Susan Stout, who opened up the resources of the Forestry Sciences Laboratory in Warren and allowed me to finish my thesis in an unfettered fashion. I thank the folks at Kane Hardwoods and Forest Investment Associates, in particular Blain Puller, Ned Karger, and Jeff Kochel for graciously allowing experimentation on their properties. This work would have been impossible without the help of many individuals who helped me census thousands of seedlings. Paula Occhuizzo provided emotional support and editorial assistance in the final stages of this work. Finally, I dedicate the entirety of this work to my children, Savanna and Ian. Their presence in my life initiated and remains the inspiration and motivation for my pursuit of professional excellence.

## TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	v
1.0 THE HERB COMMUNITY OF A TROPICAL FOREST..... IN CENTRAL PANAMÁ: DYNAMICS AND ..... IMPACT OF MAMMALIAN HERBIVORES .....	1
1.1 ABSTRACT.....	1
1.2 INTRODUCTION .....	2
1.3 METHODS .....	5
1.3.1 Research Sites .....	5
1.3.2 Experimental Design and Exclosures .....	6
1.3.3 Sampling Regime.....	6
1.3.4 Analysis.....	7
1.4 RESULTS .....	8
1.4.1 Species Richness.....	8
1.4.2 Abundance .....	9
1.5 DISCUSSION .....	9
1.5.1 On the Diversity and Abundance of Herbs in Tropical Forests.....	9
1.5.2 Mammalian Effects on Herbaceous Community .....	10
1.5.3 Long-term Consequences and Reconciliation of the Hypotheses.....	12

2.0	ON THE FORMATION OF DENSE UNDERSTORY LAYERS IN FORESTS WORLDWIDE: CONSEQUENCES AND IMPLICATIONS FOR FOREST DYNAMICS, BIODIVERSITY, AND SUCCESSION .....	20
2.1	ABSTRACT .....	20
2.2	INTRODUCTION .....	21
2.2.1	On the development of recalcitrant understory layers worldwide .....	22
2.3	PROCESSES CAUSING THE FORMATION OF RECALCITRANT UNDERSTORY LAYERS .....	24
2.3.1	Increased Overstory Disturbance .....	24
2.3.2	The interaction of elevated herbivory and canopy disturbance .....	25
2.3.3	The interaction of altered fire regimes and canopy disturbance .....	26
2.3.4	Summary .....	28
2.4	RECALCITRANT UNDERSTORY LAYERS ARREST, DELAY, AND ALTER FOREST SUCCESSION .....	28
2.4.1	Arrested Succession .....	28
2.4.2	Delayed Succession .....	29
2.4.3	Altered Gap-Phase Regeneration .....	30
2.5	MECHANISMS OF INTERFERENCE OVER TREE ESTABLISHMENT, SURVIVAL, AND GROWTH .....	30
2.5.1	Resource Competition .....	31
2.5.2	Allelopathy .....	32
2.5.3	Apparent Competition .....	33
2.5.4	Litter Accumulation .....	34
2.5.5	Mechanical Interference .....	35
2.5.6	The relationship between mechanisms of interference and phenology .....	35

2.6	ON THE CAUSES AND CONSEQUENCES OF A RECALCITRANT UNDERSTORY LAYER .....	36
2.7	IMPLICATIONS FOR FLORISTIC DIVERSITY AND FOREST SUCCESSION .....	38
2.7.1	Forest Dynamics Models .....	38
2.7.2	Forest Management.....	40
3.0	DIRECT AND INDIRECT EFFECTS OF HAY-SCENTED FERN ON TREE SEEDLINGS: A CASE FOR APPARENT COMPETITION .....	47
3.1	ABSTRACT.....	47
3.2	INTRODUCTION .....	48
3.3	METHODS .....	51
3.3.1	Research Sites .....	51
3.3.2	Understory Layer .....	51
3.3.3	Experimental Design.....	52
3.3.4	Sampling Regime.....	52
3.3.5	Statistical analysis.....	54
3.4	RESULTS .....	55
3.4.1	Small mammal activity .....	55
3.4.2	Tree seedling recruitment and establishment.....	55
3.4.3	Seed predation on different species and in different microhabitat .....	56
3.5	DISCUSSION .....	57
3.5.1	Disentangling competition from apparent competitive.....	57
3.5.2	Comparison to other studies.....	59
3.5.3	Role of post-dispersal seed predation in forest regeneration .....	62



3.5.4	Conclusion .....	62
4.0	MARCH TOWARDS MONODOMINANCE: DEER, FERN, AND THE FUTURE OF ALLEGHENY HARDWOOD FORESTS .....	71
4.1	ABSTRACT.....	71
4.2	INTRODUCTION .....	73
4.3	METHODS .....	77
4.3.1	Research Sites .....	77
4.3.2	Experimental Design.....	77
4.3.3	Sampling Regime.....	78
4.3.4	Statistical Analyses .....	79
4.4	RESULTS .....	80
4.4.1	Overstory Composition.....	80
4.4.2	Efficacy of gap treatments .....	81
4.4.3	Effects of Treatments on Emergence.....	81
4.4.4	Effects on Survival.....	82
4.4.5	Effects on Height Growth .....	82
4.4.6	Projections on cohort extinction and growth .....	83
4.4.7	Seedling layer composition and diversity .....	83
4.5	DISCUSSION .....	84
4.5.1	Seedling layer response to deer herbivory .....	84
4.5.2	Seedling layer response to fern gaps.....	85
4.5.3	Have Allegheny Forests embarked on a “March towards Monodominance”? .....	88
4.5.4	Traits conferring an advantage to black cherry in contemporary forests.....	89

4.5.5	Management Implications.....	91
BIBLIOGRAPHY .....		104

## LIST OF TABLES

Table 1.1	Herbaceous species list and mean percent cover. ....	14
Table 1.2	Repeated measures MANOVA results. ....	15
Table 1.3	Herbaceous species richness, density, and cover in various Neotropical forests. ....	16
Table 2.1	Occurrence of dense, monodominant understory species.....	44
Table 2.2	Estimates spatial coverage by recalcitrant understory layers. ....	46
Table 3.1	ANOVA Table on Germination and Survival. ....	64
Table 3.2	ANOVA table on seed preference trials. ....	65
Table 4.1	Overstory Composition.....	93
Table 4.2	Shade tolerance rankings. ....	94
Table 4.3	MANOVA results on germination and growth.....	95
Table 4.4	ANOVA table on seedling survival. ....	96
Table 4.5	MANOVA table on community-level parameters.....	97
Table 4.6	Projections times (years) on cohort extinction and growth to 1 meter. ....	98

## LIST OF FIGURES

Figure 1.1 Herbaceous species richness over time. ....	17
Figure 1.2 Herbaceous percent cover over time. ....	18
Figure 1.3 Mean herbaceous density in exclosure plots and control plots in 1994 and 1999. ....	19
Figure 2.1 Recalcitrant Understory Layer Formation.....	42
Figure 2.2 Causes and consequences of recalcitrant understory layer.....	43
Figure 3.1 Models of microhabitat-mediated apparent competition.....	66
Figure 3.2 Schematic of experimental design.....	67
Figure 3.3 Effect of small mammal predation and fern cover on germination.....	68
Figure 3.4 Effect of small mammal predation and fern cover seedling survival.....	69
Figure 3.5 Mean proportion of seeds removed by species.....	70
Figure 4.1 Schematic of split plot experimental design.....	99
Figure 4.2 Seedling emergence over time.....	100
Figure 4.3 Seedling survival of 2002 cohort.....	101
Figure 4.4 Changes in community level parameters over time. ....	102
Figure 4.5 State-Transition model. ....	103

## **1.0 THE HERB COMMUNITY OF A TROPICAL FOREST IN CENTRAL PANAMÁ: DYNAMICS AND IMPACT OF MAMMALIAN HERBIVORES**

### **1.1 ABSTRACT**

Mammals are hypothesized to either promote plant diversity by preventing competitive exclusion or limit diversity by reducing the abundance of sensitive plant species through their activities as browsers or disturbance agents. Previous studies of herbivore impacts in plant communities have focused on tree species and ignored the herbaceous community. In an experiment in mature-phase tropical moist forest sites in central Panamá we studied the impact of excluding ground-dwelling mammals on the richness and abundance of herbs in sixteen, 30 x 45 meter plots. Within each plot, we censused the herbaceous community in twenty-eight, 2 x 2 m sampling plots (1792 m<sup>2</sup> total area sampled). We identified over 54 species of herbs averaging 1.21 ramets/m<sup>2</sup> and covering approximately 4.25% of the forest floor. Excluding mammals for five years had no impact on overall species richness. Within exclosures, however, there was a significant two-fold increase in the density of rare species. Overall herbaceous density and percent cover did not differ between exclosures and adjacent control plots, although cover did increase over time. Mammalian exclusion significantly increased the total cover of three dominant herb species, *Pharus latifolius*, *Calathea inocephala*, and *Adiantum lucidum* but did not affect their density.

This study represents one of the most extensive herbaceous community censuses conducted in tropical forests and is among a few that quantify herbaceous distribution and

abundance in terms of both density *and* cover. Additionally, this work represents the first community level test of mammalian impacts on the herbaceous community in a tropical forest to date. Our results suggest that ground dwelling mammals do not play a key role in altering the relative abundance patterns of tropical herbs in the short term. Furthermore, our results contrast sharply with prior studies on similar temporal and spatial scales that demonstrate mammals strongly alter tree seedling composition and reduce seedling density. Thus, we question the pervasiveness of top-down control on tropical plant communities and the paradigm that defaunation will inexorably lead to widespread, catastrophic shifts in plant communities.

## **1.2 INTRODUCTION**

A central goal in community ecology remains disentangling and understanding the mechanisms important to the maintenance of plant species diversity. The extraordinarily high biological diversity of tropical forests has generated numerous hypotheses, stressing both biotic and abiotic factors, as explanations for the origin and maintenance of plant diversity (reviewed by Pianka 1966 and Wright 2002 among others). Prominent among these is the hypothesis that mammals, acting as seed and seedling predators, herbivores, dispersers, or disturbance agents either promote or reduce the richness and abundance of plants in tropical forests (Janzen 1970, Connell 1971, Connell 1978, Connell et al. 1984, Dirzo and Miranda 1991, Terborgh 1992, Terborgh and Wright 1994, Wright et al. 1994, Ickes et al. 2001, Roldan and Simonetti 2001, Terborgh et al. 2001, Silman et al. 2003).

It is clear that mammals often affect plant community composition and abundance through a variety of processes; however, the net effect of mammalian activity remains controversial as experimental work has yielded two diametrically opposed outcomes. On the one

hand, mammals may promote plant species diversity by preventing competitive exclusion through 1) selective foraging on seed and seedlings of dominant species, 2) increasing resource heterogeneity via physical disturbance, and 3) enhancing dispersal (Inouye et al. 1987, Huntly 1991, Kotanen 1995, Hulme 1996, Welander 2000, Willson and Traveset 2000). Alternatively, mammals may depress plant diversity via 1) indiscriminate herbivory, 2) selective browsing of rare, palatable, or uncompetitive species, and 3) trampling and uprooting during foraging activities (Milton 1940, Pacala and Crawley 1992, Arrington et al. 1999, Ickes et al 2001, Russell et al. 2001). These two views differ critically in the assumption of how competitively subordinate and/or rare plant species are affected by mammalian activity and ultimately, how this effect will influence overall plant community diversity. Specifically, the first view, predicts a rare species advantage and the maintenance of plant species diversity; the second view posits a rare species disadvantage and consequently, a decrease in diversity.

Several studies have demonstrated that mammals can greatly alter the relative abundance of plant species in forest understories. Nonetheless, the preponderance of these data focuses on shade-tolerant trees; life forms which, in time, can grow to escape the effects of ground-dwelling mammals (e.g. DeSteven and Putz 1984, Sork 1987, Terborgh and Wright 1994, Cintra 1997). This preoccupation with canopy tree species ignores the majority of the flora in tropical forests and has already led to the premature rejection of the importance of overstory gaps as a driving force structuring tropical plant communities (see Brokaw and Busing 2000 and Schnitzer and Carson 2000). We suggest that the impact of mammals on herbaceous species diversity could contrast with their effect on tree species because herbs spend their entire life cycle in the forest understory continually subject to mammalian impacts, including both herbivory and physical disturbance during foraging. Indeed, Haukioja and Koricheva (2000) concluded that the

structural, functional, and life-history characteristics inherent to many perennial herbs make them less tolerant to herbivory than woody plants. Moreover, demographic analyses suggest that herbivory may considerably depress long-term growth and reproduction of herbaceous perennials (e.g. Bierzychudek 1982, Doak 1992, Ehrlén 1995, Knight 2003). If understory species are constantly vulnerable to herbivores, they could be under strong top-down control and thus, the impact of mammals could be most pervasive and important on these life-forms (but see Feeney 1976, Grime 1977, Coley et al. 1985, and Bryant et al. 1991 for alternative view). Nonetheless, despite numerous tabulations of tropical flora worldwide, efforts to elucidate mechanisms behind the distribution, abundance, and coexistence of herbaceous species are extremely limited (but see Dirzo et al. 1992 for herbs and gaps). Furthermore, only a handful of studies have examined the prevalence and importance of mammalian impacts on herbaceous community diversity (e.g. Proulx and Mazumder 1998, Rees et al. 2001, Hambäck and Beckerman 2003). To our knowledge, the rigorous experimental work needed to determine to what degree mammals alter relative abundance patterns of tropical herb species remains nonexistent. The paucity of studies on herbaceous communities is critical as herbaceous plants represent one of the most diverse plant forms in forests (e.g. Lutz 1930, Cline and Spurr 1942, Rogers 1981, Moore and Vankat 1986, Collins and Pickett 1988). This major component of the flora also manifests itself in Neotropical forests where herbs alone can comprise from 12 to 49% of the species (Croat 1978, Gentry and Dodson 1987, Gentry 1990, Poulsen and Balslev 1991, Galeano et al. 1998, Kappelle et al. 2000).

We experimentally tested the impact of mammalian activity on the herbaceous community of a tropical forest in central Panamá by testing the following two hypotheses. First, if the net effect of ground-dwelling mammals promotes plant diversity by limiting the abundance



of competitively dominant herb species, we predict that: (i) herbaceous species richness will ultimately be lower in exclosures when compared to controls, and (ii) the density and size of the dominant herbaceous plants will be greater in experimental plots from which we exclude ground-dwelling mammals than in the unfenced control plots. Alternatively, if mammalian activity limits herbaceous diversity, we predict that: (iii) species richness should increase within exclosures relative to adjacent control plots, (iv) this increase will consist, in part, of rare species that are able to recruit into the understory when provided with protection from mammalian activity, and (v) the total density and cover of herbaceous species will be greater within exclosures than in controls. Thus, these two hypotheses make opposing predictions with regards to rare species and overall species richness and make identical predictions with regards to herbaceous species abundance.

## **1.3 METHODS**

### **1.3.1 Research Sites**

We conducted our study in the Republic of Panamá at Gigante Peninsula and Barro Colorado Island (BCI). Both sites are within the 5600 hectare Barro Colorado National Monument administered by the Smithsonian Tropical Research Institute (STRI). The forests are seasonally moist, semi-deciduous tropical forests that receive over 2.6 meters of rain/year and exhibit a marked dry season extending from January until April. The vegetation structure is typical of many other tropical forests containing a multi-tiered understory, an average canopy height of 23-30 meters, and emergent trees as tall as 50 meters (Foster and Brokaw 1996). Light levels at the forest floor are relatively dark ranging from 1.5 – 9.5 percent of full sun (Valladares et al. 2000).

Further detailed descriptions of the flora, climate, and geology of the area are found in Croat (1978) and Leigh et al. (1996).

### **1.3.2 Experimental Design and Exclosures**

In 1993, we established 8 paired 30 X 45 m plots with each pair constituting a block. Four blocks were on Gigante Peninsula and four on BCI. We randomly assigned one plot in each pair as an exclosure (fence) treatment and the other was left as an unfenced control. Within each plot we established twenty-eight, 2 X 2 m (4m<sup>2</sup>) sampling plots in a stratified random design. We included 5 – 7 m wide buffer between the perimeter of the plots and any 4m<sup>2</sup> sampling plot to allow unobstructed access and minimize any potential fence effects. The exclosure construction was completed in July 1994. The main fence was constructed with 12.7 x 12.7 cm galvanized steel fencing and extends 0.25 m below ground and approximately 2.2 m above ground. A finer 1.3 x 1.3 cm mesh fence stretches around the base of each exclosure to a depth of 25 cm and a height of approximately 70 cm. Continued monitoring and trapping has shown that the fences effectively excluded the most important ground-dwelling mammals in these forests such as agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), brocket deer (*Mazama americana*), white tail deer (*Odocoileus virginianus*), spiny rats (*Proechimys semispinosus*), peccaries (*Ayassu tajacu*), rabbits (*Silvilagus brasiliensis*) and tapirs (*Tapirus bairdii*). (Emmons and Feer 1997, Carson, unpublished data).

### **1.3.3 Sampling Regime**

Each 4m<sup>2</sup> sampling plot was censused for herbaceous species composition as well as density, and percent cover for each species. Only those ramets rooted within the plot were censused. For each individual we visually estimated cover with the aid of templates of known percent cover. Although the flora of Barro Colorado Island is one of the best studied in the Neotropics,

identification for several individuals was unfeasible due to sterile or juvenile forms or unfamiliarity. Therefore, we categorized these individuals as morphospecies. We completed the first census in May 1994 just prior to the construction of exclosures and plots were recensused in July 1999. We categorized all herbaceous species from rare to abundant following Croat's Flora of Barro Colorado Island (1978) categorizations. Additionally, for our analyses, we considered the lowest 5% of the species or morphospecies on a rank abundance curve of total number of individuals as rare.

We conducted a number of tests to examine changes in the plant community parameters of richness, density, and cover. In addition, we focused on changes in density and cover in three dominant plants: *Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*. Not only are these three species designated as abundant or common in the Flora of Barro Colorado (Croat 1978), moreover these three species together accounted for approximately one-third of the total cover and number of ramets sampled at the start of the experiment and were represented in all plots. Although two other species, *Philodendron inaequilaterum* and *Tectaria incisa*, were also abundant, their distribution was extremely patchy. For these two species it did not make sense to explore the effects of mammal suppression between treatments or over time as they were absent from a large number (25 – 44%) of plots. The inclusion of such a large number of zero values would highly skew the data and create high plot-to-plot variability, thus violating the assumptions of ANOVA (Carson and Root 1999).

#### **1.3.4 Analysis**

For all analyses, we used multivariate repeated-measures analysis of variance (rmMANOVA) where the response variables for each time period (1994 & 1999) were treated as different dependent variables. This procedure is the most robust test for time series data as it controls for

the correlation between dates and the resulting lack of independence within replicates (von Ende 2001). The between subject factors were block and treatment (Exclosure/Control); within subject factors were year, year x block, and treatment x year interactions. The treatment x year interaction is the decisive test to determine whether any changes observed over time differ between control plots and exclosure plots (von Ende 2001). Statistical tests exploring the effect of the treatments on richness (number of species) utilized the total number of species for all 28 sampling plots per plot. For analyses on the community level parameters of density and percent cover, we used the average of the parameter across all twenty-eight sampling plots within a plot. As our predictions for rare species density and dominant species density and cover are directional, we report the one-tailed p-values. We assessed normality using the Shapiro Wilk test (Shapiro & Wilk 1965) and applied the arcsine transformation to percent cover data only when needed (Sokal and Rohlf 1995).

## **1.4 RESULTS**

### **1.4.1 Species Richness**

We censused 2116 and 2206 ramets in 1994 and 1999, respectively. The average density ranged from 1.17 – 1.26 ramets m<sup>-2</sup>. We recognized 62 different herbs and were able to identify 89% of them to either species or genus level (Table 1.1). The results demonstrate that this flora is typical of similar diverse systems comprised of few abundant species and many rare ones. The censuses demonstrate that four species (6.5%) account for over 50% of the total number of ramets; conversely, forty species (64.5%) comprise the lowest 5% of the total number of ramets.

Overall species richness was significantly greater within exclosures ( $F = 7.88$ ,  $p = .026$ ). Indeed, the data indicate an increase from a mean of 14.625 species in 1994 to 16.75 species in 1999 (a 14.5% increase) in the exclosures, whereas the controls increased from 12.125 species in

1994 and 13.125 species in 1999 (Figure 1.1). Nonetheless, species richness was highest in the exclosures even at the start of the experiment and the repeated measures analysis confirms that the slight differences between the exclosures and controls in species richness over time are not significant (treatment x year;  $F = 2.97$ ,  $p = .129$ ). Thus, the data demonstrate that mammalian activity had no significant effect on overall species richness (Table 1.2, Figure 1.1).

#### **1.4.2 Abundance**

We found no significant effect of excluding mammals on total cover or total plant density. Total herbaceous percent cover (but not density) increased significantly over time in both treatments (Table 1.2; Figures 1.2a & 1.3a).

Excluding mammals significantly increased the cover of the dominant forest herbs (*Adiantum lucidum*, *Calathea inocephala*, *Pharus latifolius*) by 65% (Figure 1.2b). Although the cover of this group of herbs increased in both controls and exclosures over time, the significant treatment x year interaction reveals that the increase within the exclosures was significantly greater than the increase in the control plots (Table 1.2; Figure 1.2b). Removal of mammals for five years had no effect on density of dominant species as indicated by the treatment x year term (Table 1.2; Figure 1.3b).

Finally, excluding mammals for five years resulted in a significant increase in density of the rarest forty species (treatment x year interaction;  $F = 5.16$ ,  $p = 0.0285$ ) resulting in two-fold greater densities when compared to the adjacent control plots (Figure 1.3c).

### **1.5 DISCUSSION**

#### **1.5.1 On the Diversity and Abundance of Herbs in Tropical Forests**

Despite Gentry and Dodson's 1987 paper emphasizing the substantial contribution of non-tree species to the overall plant diversity of tropical forests, there remains a paucity of studies

characterizing the distribution and abundance of neotropical herbaceous communities. In fact, a literature search for work comparable to ours using the Agricola and Biological Abstracts databases as well as the literature citations of identified papers yielded only eight studies at twelve additional sites for which both herb richness and abundance (density or cover) was tallied (Table 1.3). Even among these studies there is considerable variation with respects to sampling effort and design, sampling location (e.g. understory vs. gap), and categorizations of herbaceous lifeforms. Given the suite of limitations, we find cross-site comparisons and synthesis inadequate, if not impossible, due to a lack of methodological standardization. Nevertheless, we do find that herb cover tends to increase with annual precipitation; however, this increase is predominantly due to a rise in dominance of large-leafed palms and monocots and not an increase overall stem density (Table 1.1 & 1.3; Gentry 1990, Montgomery 2004). In fact, across most forested sites, herbaceous density is generally low ( $1 - 2$  ramets/m<sup>2</sup>) and increases greatly only within gaps and in more open, semi-deciduous forests (Table 1.3). Despite these broad generalizations, we suggest quantitative work on tropical herb communities is still in its infancy and true synthesis will require a concerted effort by researchers employing standardized measures across multiple sites.

### **1.5.2 Mammalian Effects on Herbaceous Community**

Several authors have recently warned that changes in the mammalian fauna could lead to ‘catastrophic’ or ‘revolutionary’ shifts in plant species composition (Dirzo and Miranda 1991, Terborgh et al. 2001, Silman et al. 2003, Wright 2003). Despite these warnings, our results do not justify these assertions. After five years of mammal removal, the herbaceous community did not exhibit marked increases or decrease in species richness, overall percent cover, or density. The two-fold increase in rare species density within fenced plots suggests that mammalian

activity does limit the abundance of some plant species. This finding is consistent with other studies reporting an increase in rare species following release from mammals (e.g. Edwards and Crawley 1999, Cabin et al. 2000, Donlan, et al. 2002). Whether or not these species originated from the seed bank or via outside dispersal is unknown. Although dispersal may be limited within the fenced plots by the exclusion of the ground-dwelling mammalian fauna, several other dispersal vectors which are not constrained by the fences remain (e.g. wind, water, arboreal mammals, birds, and insects; Beattie and Culver 1981, Lu and Mesler 1981, Howe and Smallwood 1982, Horvitz 1991, Stiles 2000, McLachlan and Bazely 2001, Pizo and Morellato 2002).

The expansion in dominant herb species cover following release from ground-dwelling mammals suggests that mammalian activity may limit the abundance of these species. This result is consistent with prior studies reporting increases in abundance of a subset of plant species following mammalian exclusion or defaunation (e.g. Brown and Heske 1990, Dirzo and Miranda 1990, Bowers and Sacchi 1991, Gutierrez et al. 1997, Ritchie et al. 1998). We propose that the most likely explanation for the expansion of a few dominants is the absence of herbivory and physical disturbance by ground-dwelling mammals. In tropical forest understories, there is ample evidence that mammalian seed and seedling predation strongly reduces the abundance of many woody species (e.g. Clark and Clark 1989, Hammond and Brown 1998). Although to date analogous experiments have not been performed on non-woody plant species (Schupp et al. 1989), existing data confirms that mammalian diets include herbs (Terwilliger 1978, Robinson and Redford 1986, Brooks et al. 1997, Tobler 2002). Additionally, non-trophic interactions, including uprooting and trampling, cause considerable damage to understory vegetation and potentially alter species composition (Clark and Clark 1989, Arrington et al. 1999, Ickes et al.

2001, Gillman and Ogden 2003). Thus, either through direct consumption or non-trophic interactions, mammals could potentially limit the abundance of herbaceous species.

### **1.5.3 Long-term Consequences and Reconciliation of the Hypotheses**

Our data seemingly reveal a paradox between increasing cover of the three dominant species in conjunction with increases in rare species density. We propose that the existence of a time lag is a likely explanation that will reconcile this apparent paradox. Specifically, we suggest that competitive exclusion by dominant competitors is not instantaneous, particularly in the light-limited forest understory, and that this lag could allow a transient recruitment opportunity for rare species that will ultimately wane as the dominant plants continue to expand and overtake space though this dynamic may require decades to play itself out. Such lagged responses to herbivore removal experiments are common in herbaceous communities and their existence clearly highlights the importance of long-term research in plant communities (e.g. Carson and Root 2000, Brown et al 2001, Rees et al. 2001). Alternatively, the increases in recruitment of rare species inside exclosures may prove robust providing solid support that mammalian activity limits plant diversity in tropical understories. However, the strongest evidence for the concept that mammals exert strong top-down control on plant diversity comes from communities with overabundant mammal populations (e.g. Donlan et al. 2002, Terborgh et al. 2001). At BCI the existing data does not support the assumption of excessively high mammal abundances (Wright et al. 1994, Wright et al. 2000), making this alternative unlikely.

Our results are likely a conservative measure of the effects of mammals on the ground flora. Wright (2002) hypothesized that low understory plant abundances may negate the existence of competition in tropical forests. Furthermore, he predicted competition would only become important when understory plant abundance increased following, among other factors,



release from herbivores. Although the BCI herbaceous layer is as speciose as other neotropical forests (Gentry 1990), the herbaceous layer is relatively sparse relative to wetter tropical forests. If Wright's prediction proves correct, release from mammalian in forests containing these dense initial conditions may allow competitive exclusion to proceed at a greatly accelerated pace. Thus, although the results of this experiment demonstrate that mammals are not the major force structuring the understory herbaceous communities of semi-deciduous tropical forests, clearly, further experimentation is required to assess the scope and generality of their effects.

**Table 1.1 Herbaceous species list and mean percent cover.**

Herbaceous species list and mean percent cover (%cover/4m<sup>2</sup>;  $\pm 1$  SE) for each treatment (Controls and Exclosures) at each census period along with abundance classifications (see text for explanation). Cover estimates represent the grand mean across all eight plots within a treatment. Asterisks (\*) denote cover estimates < 0.005%, hyphens (-) indicate absence of species.

Species	Abundance	Croat	Control				Fence			
			1994	SE $\pm$	1999	SE $\pm$	1994	SE $\pm$	1999	SE $\pm$
<i>Adiantum lucidum</i>	Abundant	5	0.34	0.09	0.41	0.09	0.46	0.07	0.57	0.11
<i>Adiantum obliquum</i>	Rare	3	0.01	0.01	0.01	0.01	*	*	*	*
<i>Adiantum petiolatum</i>	Common	4	0.03	0.03	0.04	0.04	0.03	0.02	0.01	0.01
<i>Aechmea magdalenae</i>	Abundant	5	0.17	0.16	0.14	0.14	0.12	0.11	0.17	0.17
<i>Anthurium</i> spp.	Rare	-	*	*	-	-	-	-	-	-
Araceae	Rare	-	-	-	-	-	-	-	0.02	0.01
Araceae1	Rare	-	-	-	-	-	-	-	*	*
Araceae2	Rare	-	-	-	*	*	-	-	-	-
<i>Asplenium delitescens</i>	Rare	3	*	*	*	*	-	-	-	-
<i>Calathea inocephala</i>	Common	4	0.22	0.08	0.60	0.18	0.60	0.14	1.27	0.24
<i>Calathea insignis</i>	Rare	1	-	-	-	-	*	*	-	-
<i>Calathea latifolia</i>	Rare	2	-	-	-	-	-	-	*	*
<i>Calathea micans</i>	Rare	4	-	-	*	*	-	-	0.01	0.01
<i>Calathea</i> spp.	Rare	-	-	-	0.03	0.03	-	-	0.15	0.15
<i>Chusquea simpliciflora</i>	Rare	5	0.01	0.01	*	*	*	*	-	-
<i>Costus</i> spp.	Rare	-	0.02	0.02	0.04	0.03	0.02	0.02	0.04	0.03
<i>Dennstaedtia cicutaria</i>	Rare	1	0.08	0.08	0.05	0.05	-	-	-	-
<i>Dictyoxiphium panamense</i>	Rare	4	0.05	0.05	0.03	0.03	-	-	-	-
<i>Dieffenbachia longispatha</i>	Common	4	0.47	0.26	0.88	0.46	0.23	0.11	0.27	0.13
<i>Dieffenbachia oerstedii</i>	Rare	4	-	-	*	*	-	-	-	-
<i>Dieffenbachia pittieri</i>	Occasional	3	0.01	0.01	0.07	0.07	0.02	0.01	0.04	0.03
<i>Dieffenbachia</i> spp.	Rare	-	-	-	-	-	-	-	0.03	0.03
<i>Diplazium grandifolium</i>	Rare	5	-	-	-	-	*	*	-	-
<i>Dioscorea</i> spp.	Rare	-	*	*	*	*	0.01	0.00	0.01	0.01
<i>Geophila croatii</i>	Rare	3	-	-	-	-	*	*	0.01	0.01
<i>Geophila repens</i>	Rare	4	-	-	-	-	0.14	0.14	0.14	0.14
Unknown Grass	Rare	-	-	-	-	-	*	*	-	-
<i>Heliconia</i> spp.	Rare	-	0.03	0.03	*	*	0.01	0.01	0.13	0.07
<i>Ischnosiphon pruinusos</i>	Common	4	0.04	0.04	0.06	0.06	0.13	0.10	0.07	0.07
<i>Lomariopsis vestita</i>	Rare	4	-	-	-	-	-	-	0.01	0.01
<i>Lygodium radiatum</i>	Rare	3	0.01	0.01	*	*	0.03	0.03	*	*
<i>Monstera dilacerata</i>	Infrequent	2	0.04	0.02	0.09	0.05	0.05	0.02	0.26	0.08
<i>Monstera dubia</i>	Rare	4	-	-	*	*	0.01	0.00	0.01	0.01
<i>Monstera</i> spp.	Rare	-	-	-	-	-	*	*	-	-
Maranthaceae	Rare	-	-	-	-	-	-	-	0.03	0.03
<i>Olyra latifolia</i>	Common	4	0.03	0.03	0.01	0.01	0.22	0.20	0.12	0.12
<i>Pharus latifolius</i>	Abundant	5	0.33	0.11	0.49	0.11	0.55	0.20	0.79	0.16
<i>Pharus parvifolius</i>	Rare	3	-	-	0.03	0.03	0.12	0.12	0.54	0.54
<i>Pharus</i> spp.	Rare	-	-	-	-	-	-	-	0.02	0.02
<i>Philodendron fragrantissimum</i>	Rare	4	*	*	-	-	-	-	-	-
<i>Philodendron guttiferum</i>	Abundant	5	0.22	0.07	0.32	0.15	0.10	0.04	0.19	0.09
<i>Philodendron inaequilaterum</i>	Abundant	5	0.77	0.30	0.92	0.43	0.59	0.28	0.86	0.44
<i>Philodendron</i> spp.	Rare	-	-	-	*	*	-	-	0.03	0.03
<i>Polypodium pectinatum</i>	Rare	5	-	-	-	-	0.01	0.01	-	-
<i>Scleria</i> spp.	Rare	-	-	-	-	-	0.03	0.02	-	-
<i>Selaginella arthritica</i>	Abundant	5	0.11	0.08	0.10	0.06	0.25	0.21	0.27	0.22
<i>Spathiphyllum friedrichsthalii</i>	Rare	4	0.01	0.01	-	-	0.05	0.04	0.10	0.07
<i>Spathiphyllum phrynifolium</i>	Rare	3	-	-	0.02	0.02	-	-	-	-
<i>Streptogyne americana</i>	Common	4	-	-	*	*	-	-	0.05	0.04
<i>Streptochaeta sodiroana</i>	Common	4	0.02	0.01	0.04	0.03	0.06	0.04	0.06	0.04
<i>Streptochaeta spicata</i>	Occasional	3	0.29	0.28	0.34	0.30	0.04	0.02	0.07	0.04
<i>Stromanthe jacquinii</i>	Infrequent	2	-	-	-	-	0.23	0.23	0.18	0.18
<i>Syngonium erythrophyllum</i>	Common	4	*	*	0.05	0.02	0.01	0.01	0.07	0.02
<i>Syngonium podophyllum</i>	Rare	5	*	*	-	-	*	*	-	-
<i>Syngonium</i> spp.	Rare	-	*	*	-	-	-	-	0.01	0.00
<i>Tectaria incisa</i>	Abundant	5	0.72	0.41	1.11	0.70	0.61	0.34	1.15	0.52
<i>Thelypteris nicaraguensis</i>	Abundant	5	0.11	0.05	0.09	0.04	0.04	0.02	0.06	0.02
<i>Thelypteris poitaena</i>	Rare	4	*	*	*	*	-	-	-	-
Unknown	Rare	-	-	-	0.06	0.06	-	-	0.03	0.03
<i>Xanthosoma pilosum</i>	Rare	5	*	*	-	-	-	-	-	-
<i>Xiphidium caeruleum</i>	Rare	4	-	-	-	-	*	*	-	-
Zingiberaceae	Rare	-	-	-	0.01	0.01	-	-	-	-
<b># of Species</b>			34		39		38		42	
<b># of Ramets</b>			1054		1062		1123		1083	

**Table 1.2 Repeated measures MANOVA results.**

Repeated measures MANOVA results for the effects of ground-dwelling mammal exclosures on richness (# of species), density (#ramets/m<sup>2</sup>), and percent cover of the entire herbaceous community as well as the combined density and percent cover of the three dominant herbs: *Adiantum lucidum*, *Calathea inocephala*, & *Pharus latifolius*.

Response	Between Plot analysis over all years			Within Plot Analyses					
	Treatment Effects			Year Effects			Treatment x Year		
	df	F	P	df	F	P	df	F	P
Richness	1,7	7.88	0.026	1,7	17.08	0.004	1,7	2.97	0.129
Total Cover (%)	1,7	4.65	0.068	1,7	53.92	<0.001	1,7	3.04	0.125
Total Density (#/m <sup>2</sup> )	1,7	0.17	0.696	1,7	0.17	0.696	1,7	0.30	0.599
Rare Species Density <sup>a</sup>	1,7	1.92	0.104	1,7	1.55	0.252	1,7	5.16	0.029
Cover of Dominants <sup>a</sup>	1,7	18.83	0.001	1,7	85.25	<0.0001	1,7	5.63	0.025
Density of Dominants <sup>a</sup>	1,7	8.3	0.012	1,7	3.66	0.099	1,7	2.52	0.079

<sup>a</sup> The predictions for these response variables are directional and justify one-tailed tests. Therefore the p-values for treatment and treatment x year represent one-tailed probabilities.

**Table 1.3 Herbaceous species richness, density, and cover in various Neotropical forests.**

Herbaceous species richness (# of species), density (#ramets/m<sup>2</sup>), and percent cover, in various Neotropical forests.

Author(s)	Location	Coordinates	Mean Annual Rainfall (mm)	Area Sampled	Terrestrial Herbs	Climbers <sup>b</sup>	Mean density (# m <sup>-2</sup> )	Mean Cover
Gentry and Dodson (1987)	Capeira, Ecuador	2° 0'S, 79° 53 'W	804	1000 m <sup>2</sup>	50	58	2.85	-
Killeen et al. (1998)	Lomerío, Bolivia	16° 13 'S, 61° 50 'W	1129	1600 m <sup>2</sup> <sup>a</sup>	55	38	6.9	-
Gentry and Dodson (1987)	Jauneche, Ecuador	1° 18 'S, 79° 35 'W	1850	1000 m <sup>2</sup>	18	58	~1.0	-
Fujisaka et al. (1998)	Amazonia, Brazil	9° 53 'S, 67° 49 'W	2000	240 m <sup>2</sup>	~24	~40	~2.0	-
Poulsen and Baslev (1991)	Cuyabeno, Ecuador	00° 00 'S, 76° 12 'W	2479 - 3244	10000 m <sup>2</sup>	57	26	~1.0	2.5% of total area
Royo & Carson	BCI, Panama	9° 09 'N, 79° 51 'W	2600	1792 m <sup>2</sup>	47	13	~1.21	~ 4.25%
Gentry and Dodson (1987)	Río Palenque Ecuador	0° 32 'S, 79° 25 'W	2980	1000 m <sup>2</sup>	50	36	1.22	-
Mayfield and Daily ( <i>in press</i> )	Las Cruces, Costa Rica	8° 47' N, 82° 57' W	4000	120 m <sup>2</sup>	26	25	6.05	-
Royo & Carson ( <i>unpub. data</i> )	La Selva, Costa Rica	10° 26 'N, 83° 59 'W	4000	960 m <sup>2</sup>	25	17	2.88	13.90%
Whitmore et al. (1985)	Horquetas, Costa Rica	10° 22 'N, 84° 05 'W	4000	100 m <sup>2</sup>	16	21	1.12 - 3.52 <sup>c</sup>	-
Dirzo et al. (1992)	Los Tuxtlas, Mexico (Gaps)	18° 34 'N, 95° 04 'W	4700	20 m <sup>2</sup>	8	7	13.4	27%
Mayfield and Daily ( <i>in press</i> )	La Palma, Costa Rica	8° 40' N, 83° 27' W	5000	120 m <sup>2</sup>	22	16	5.4	-
Mayfield and Daily ( <i>in press</i> )	Pto. Jimenez, Costa Rica	8° 31' N 83° 19' W	5000	120 m <sup>2</sup>	18	12	3.5	-
Galeano et al. (1998)	El Amargal, Columbia	5° 29' - 6° 08' N, 77° 10' - 77° 32' W	7150	1000 m <sup>2</sup>	63	21	1.87	-

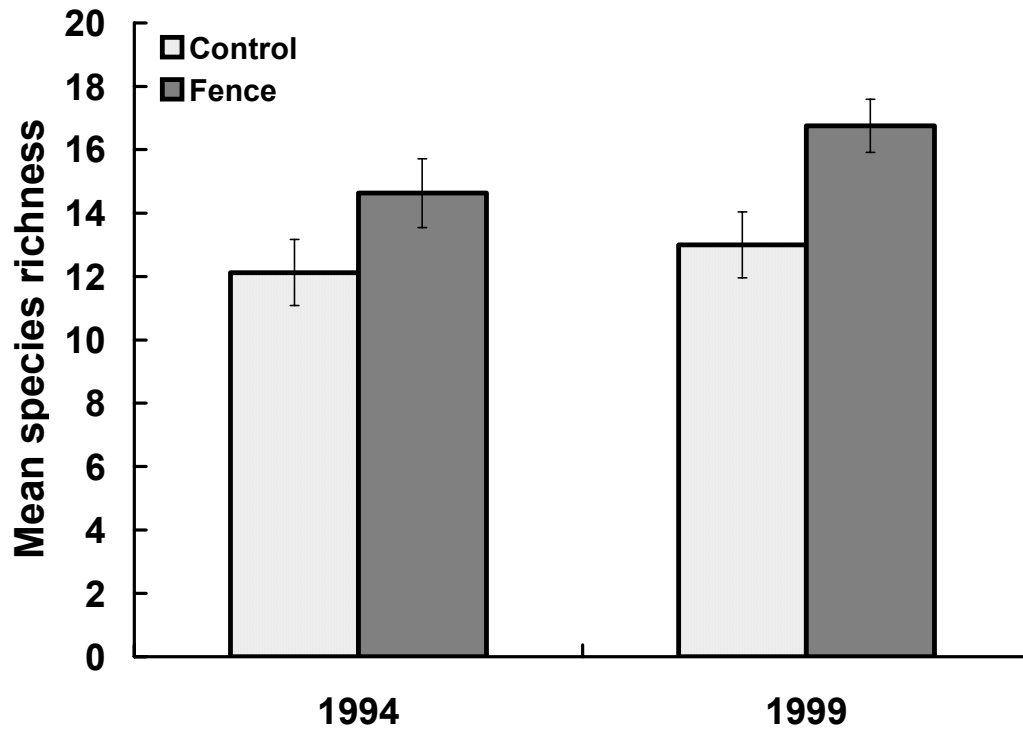
<sup>a</sup> Used Nested subplot design of various plot sizes, for forest floor flora (< 2 m tall and < 5 cm dbh) area sampled was 1600 m<sup>2</sup>

<sup>b</sup> Climbers category may include hemiepiphytes, herbaceous climbers, and woody climbers.

<sup>c</sup> Lower estimate is density of free-standing herbs, higher estimate includes herbaceous climbers

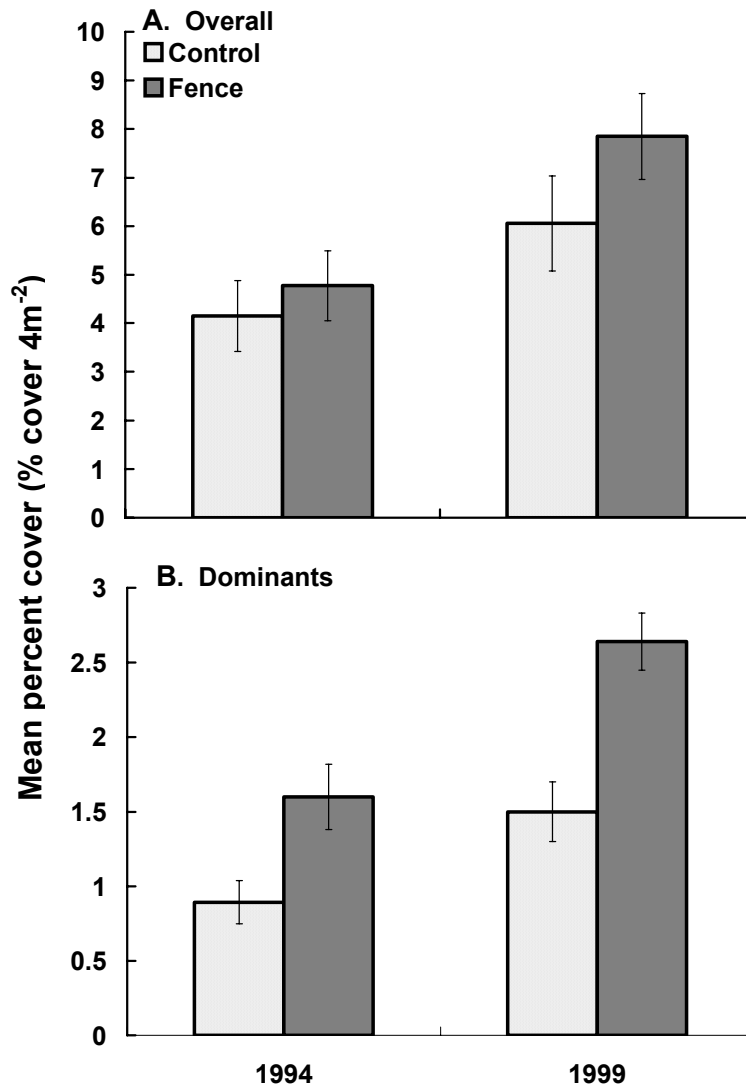
**Figure 1.1 Herbaceous species richness over time.**

Species richness (# species per plot) for herbaceous plants (mean  $\pm$  1 SE) in exclosure plots and control plots in 1994 and 1999.



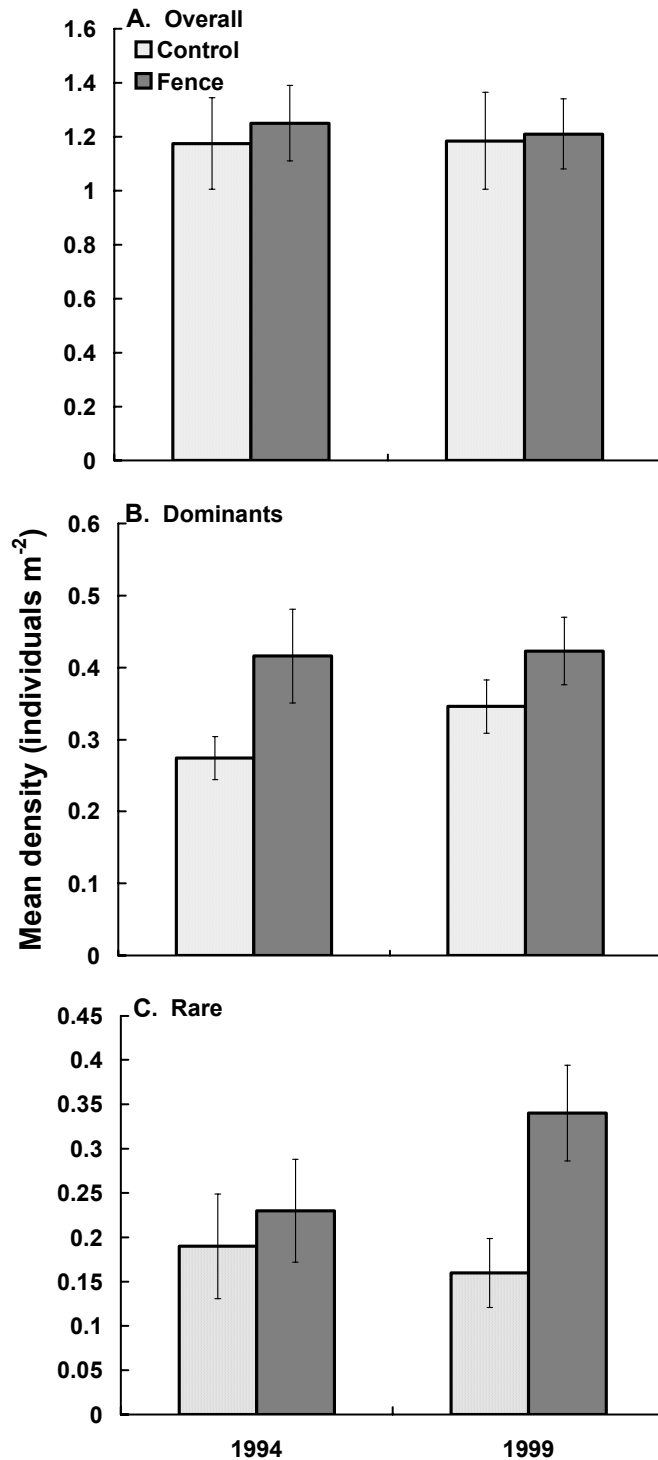
**Figure 1.2 Herbaceous percent cover over time.**

Mean herbaceous percent cover (%cover  $4\text{m}^{-2}$ ;  $\pm 1$  SE) in exclosure plots and control plots in 1994 and 1999 **a)** overall herbaceous cover, **b)** dominant herbaceous species as a group (*Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*).



**Figure 1.3 Mean herbaceous density in exclosure plots and control plots in 1994 and 1999.**

Mean herbaceous density (# of ramets  $\text{m}^{-2}$ ;  $\pm 1$  SE) in exclosure plots and control plots in 1994 and 1999 **a)** overall herbaceous density, **b)** dominant herbaceous species as a group (*Adiantum lucidum*, *Calathea inocephala*, and *Pharus latifolius*), **c)** rare species.



## **2.0 ON THE FORMATION OF DENSE UNDERSTORY LAYERS IN FORESTS WORLDWIDE: CONSEQUENCES AND IMPLICATIONS FOR FOREST DYNAMICS, BIODIVERSITY, AND SUCCESSION**

### **2.1 ABSTRACT**

The mechanistic basis underpinning forest successional models is the gap-phase paradigm in which variation in size and frequency of overstory disturbance interacts with the shade tolerance of suppressed seedlings and saplings to determine successional trajectories. The theory, and ensuing forest simulation models, typically ignore all interactions that occur prior to gap formation and assume that understory herbs and shrubs have little impact on the composition of the advance regeneration layer. This review challenges those assumptions by bringing together over 125 papers on 38 understory species that form nearly monodominant, impenetrable, and persistent understory canopies in forests worldwide. Once established, this vegetation layer strongly diminishes tree seedling recruitment, growth, and survival rates, thus slowing the rate and altering the outcome of forest succession. We term these dense strata recalcitrant understory layers.

We found the formation of these recalcitrant understory layers was linked to alterations to the disturbance and herbivory regimes in forests. Specifically, in over half of the examples we examined, disturbances that opened up the canopy interacted with either increased herbivory or altered fire regimes to create novel conditions that favor only a small subset of understory species. These species typically spread vegetatively, are fast-growing, relatively shade-



intolerant, fire-tolerant, and herbivore-tolerant. In nearly three fourths of the species examined, resource competition and allelopathy were suggested as the likely interference mechanisms decreasing tree regeneration. However, we also found that only one quarter of the published studies rigorously tested the putative interference mechanisms using manipulative field experiments. Of this limited set, above- and belowground competition and allelopathy were tested in 37, 32, and 13% of the cases, respectively. These data suggest that a basic understanding of the mechanistic basis underlying the interference lags behind its phenomenological characterization.

We summarize the causes and consequences of recalcitrant understory layers in a conceptual model that links the factors predisposing their formation, their various interference mechanisms, and subsequent impacts on forest successional dynamics. We propose that the formation of such a layer further constricts floristic diversity and contributes to the homogenization of forest systems. Furthermore, we argue that these novel understory strata should be explicitly considered in forest dynamics theory and simulation models as their presence may profoundly alter successional outcomes. Finally, we offer some management suggestions to limit the establishment of recalcitrant understory layers and mitigate their negative impacts on regeneration.

## **2.2 INTRODUCTION**

Current forest successional theory focuses primarily on the processes that occur after major disturbances, particularly species recruitment, growth, survivorship, and turnover (Watt 1947, Bray 1956, Runkle 1981, 1982, Uhl et al. 1988, Houle 1990, Oliver and Larson 1996, Marks and Gardescu 1998, Greene et al. 1999, Antos et al. 2000, McCarthy 2001; see also *Ecology* Special

Feature Vol. 70 1989, *Biotropica* Special Feature Vol. 28 1996). This theory typically assumes that (1) the advanced regeneration layer is diverse and composed of a well-developed seedling and sapling layer, (2) tree species vary in shade-tolerance, (3) overstory disturbances vary in size and frequency, and (4) variation in these disturbances and the degree of shade-tolerance interact to determine successional trajectories (eg. SORTIE Forest Dynamics Model; Kobe et al 1995, Pacala et al. 1996). This theoretical framework rarely considers or neglects the processes structuring the advanced regeneration layer prior to overstory gap formation (Connell 1989, Runkle 1990, Hill 1996, Connell et al. 1997). In addition, this view of forest succession assumes that the rest of the understory community (herbs and shrubs) has little impact on post-disturbance tree species regeneration and subsequent canopy formation (Ehrenfeld 1980). In contrast, we present evidence the herb and shrub layer can act as a strong filter on tree species succession both after a major canopy disturbance and prior to any disturbance within closed canopy forests (Runkle 1990). We agree with Connell (1989) that, “the selection that takes place beneath the closed canopy has a great influence of the suite of species available to take advantage...of a gap” and thus reach the canopy.

### **2.2.1 On the development of recalcitrant understory layers worldwide**

Recent changes in disturbance and browsing regimes have strongly impacted species composition in forest understories worldwide (de la Cretaz and Kelty 1999, Vandermast et al. 2002, Coomes et al. 2003, Mallik 2003). Typically, these changes have led to large increases in the density and cover of a small number of understory plant species (e.g. Mallik 2003). In many cases, these species expand to form persistent, monodominant layers that, in some cases, are nearly impenetrable (Figure 2.1, Tables 2.1 & 2.2). We term these dense strata Recalcitrant Understory Layers. No matter where they occur worldwide, they have a number of attributes in

common. (1) The understory layer is often more dense with greater vegetation cover and lower diversity than was common in forest understories in the past. (2) This layer alters successional trajectories and slows the rate of succession by creating conditions in the understory near ground level that are inimical to seeds and seedlings of many tree species (e.g., very low light at the soil surface). (3) Once this layer is formed it can resist displacement by other species and remain intact for decades even beneath closed canopy forests. These layers and species have been termed Low Canopies (Schnitzer et al. 2000) and Native Invasives, respectively (de la Cretaz and Kelty 1999). We prefer recalcitrant understory layer because it emphasizes that the effect of this layer occurs in the understory and is resistant to displacement. Additionally, the term native invasive suggests these species are invading novel habitat when in fact the species that formed these layers were present throughout the habitat at varying degrees of abundance. Overall, we argue that models and theories of forest succession must now consider that many forests have a strong understory filter which determines which tree species are present to take advantage of a newly formed gap. In many cases, these recalcitrant understory layers are dramatically altering forest wide species diversity and patterns of succession.

In this paper, we first review the processes that cause the formation of recalcitrant understory layers. Second, we describe how these layers alter the rate and direction of forest succession. Third, we review published work to identify how these layers control tree recruitment, growth, and survivorship and thus patterns of tree regeneration and succession. Fourth, we present a conceptual model that synthesizes identifies the most prominent causal mechanisms for the formation of these layers, outlines the consequences of their formation on successional dynamics and forest regeneration. Finally, we discuss how recalcitrant understory

layers may reduce floristic diversity, we argue for their incorporation into forest successional models, and we explore management options for mitigation of their impacts.

## **2.3 PROCESSES CAUSING THE FORMATION OF RECALCITRANT UNDERSTORY LAYERS**

### **2.3.1 Increased Overstory Disturbance**

In the past century, large-scale disturbances including logging, fires, insect outbreaks, and pathogens have increased the extent and particularly the frequency of overstory disturbance (Sharitz et al. 1992, Youngblood and Titus 1996, Seymour et al. 2002, Carson et al. 2004). These disturbances increase resource availability (e.g., light) in the understory both in the short term and over many successive years. There is little doubt that these disturbances increase the establishment and growth of seedlings and saplings of canopy trees at least in the short term (Hartshorn 1978, Runkle 1982, Denslow 1987, Canham 1989, Canham et al. 1994, Finzi and Canham 2000). However, these extensive and repeated overstory disturbances may be most beneficial to a few understory species that possess high rates of growth and vegetative expansion when exposed to high light (Ehrenfeld 1980, Huenneke 1983, Schnitzer et al. 2000; Table 2.1). These species are typically shade-intolerant, yet highly plastic, so that they can persist at low light levels following canopy closure by utilizing sunflecks or clonal integration (e.g. Lipscomb and Nilsen 1990, Messier 1992). (Brach et al. 1993, Moola and Mallik 1998).

There are numerous examples worldwide whereby canopy disturbances lead to the formation of recalcitrant understory layers (Table 2.1). Gerwing (2001) found that logging caused the formation of a dense understory tangle of lianas, which retarded canopy formation in Amazonia. Throughout the tropics, large-scale disturbances can create bamboo and fern thickets that persist for decades (Guarigauta 1990, Walker 1994, Russell et al. 1998, Griscom & Ashton

2003). In temperate and boreal forests, both native and exotic outbreaking insects open up vast areas of forest canopies (e.g., Gypsy moth *Lymantria dispar* and Spruce budworm *Choristoneura fumiferana*) often leading to an increase in the density and dominance of a few shrub species (Ghent et al. 1957, Ehrenfeld 1980, Batzer and Popp 1985, Hix et al. 1991, Muzika and Twery 1995, Aubin et al. 2000). Fungal pathogens can open up canopies in central New York (Dutch elm disease, *Ophiostoma ulmi*) causing the formation of widespread and dense patches of *Alnus*, *Cornus*, and *Viburnum* spp.. (Huenneke 1983). Both Huenneke (1983) and Ehrenfeld (1980) argued that these dense shrub layers would delay canopy formation and alter its composition. Likewise, Chestnut blight (*Cryphonectria parasitica*) apparently led to the aggressive expansion of *Rhododendron maximum* in the southern Appalachians (Vandermaast et al. 2002). In general, any process, whether anthropogenic or not, that increases light availability in the understory has the potential to lead to the formation of recalcitrant understory layers. Nonetheless, it appears that several processes must be altered in combination before these recalcitrant layers can form (see below).

### **2.3.2 The interaction of elevated herbivory and canopy disturbance**

In many parts of the world, large-scale canopy disturbances have coincided with extended periods of elevated browsing by either introduced or native mammalian herbivores (e.g. white-tailed deer in eastern U.S.; reviewed by McShea et al. 1997, Russell et al. 2001). Years of heavy browsing can lead to depauperate understories composed almost entirely of highly browse tolerant or unpalatable species (e.g. Waller and Alverson 1997, Rooney and Dress 1997, Horsley et al. 2003, Banta et al. 2005). If these browse tolerant or unpalatable species happen to be clonal shrubs or herbs, then any canopy disturbance that suddenly elevates understory light levels can cause the rapid expansion of these species. One of best examples of the interplay between

long periods of overbrowsing and canopy disturbance is where hay-scented fern (*Dennstaedtia punctilobula*) has formed a recalcitrant understory layer throughout Pennsylvania and other parts of the northeast US (De la Cretaz and Kelty 1999). Essentially, years of overbrowsing cleaned out the understory. When light levels increased, hay-scented fern rapidly spread into this sparsely occupied habitat forming dense monospecific stands (Fig. 1). Other examples include Sweden where clearcutting and overbrowsing convert forests to unpalatable grass-dominated communities (e.g. *Deschampsia flexuosa*; Bergquist et al. 1999) and New Zealand where arboreal herbivory by marsupials opens up the canopy and in combination with overbrowsing by deer leads to stands of unpalatable ferns and shrubs (Jane and Pracy 1974, Allen et al. 1984, Rogers and Leathwick 1997, Wardle et al. 2001, Coomes et al. 2003).

### **2.3.3 The interaction of altered fire regimes and canopy disturbance**

Humans have either substantially decreased or increased the frequency or severity of fire in various ecosystems (Attiwill 1994, May 2000, Mallik 2003). Frequent fires thin the understory by reducing seedling and sapling density thereby increasing light availability; this favors species that can survive the fire or resprout thereafter (Abrams 1992, Collins and Carson 2003, Donlan and Parker 2004). When canopy disturbances and fires occur in tandem or within a relatively short period the increase in light can contribute to the development recalcitrant understory layer (Mallik 2003, Payette and Delwaide 2003). For example, in boreal forests Payette and Delwaide (2003) found that a “synergy” existed between fire and overstory disturbance, which created shrub-dominated heathlands. These heathlands became dominated by shrubs species, mainly *Calluna*, *Kalmia*, and *Vaccinium* spp., which can rapidly resprout and spread clonally following fires (Meades 1983, Mallik 1995). Similarly, catastrophic fires in tropical forests can generate dominance by shade-intolerant ferns (*Dicranopteris*, *Gleichenia*, or *Pteridium* spp) or bamboo

(*Guadua*) that also spread clonally following fires (Gleissman 1978a, Dolling 1999, Nelson 1994, May 2000).

Alternatively, canopy disturbances that coincide with a decrease in fire frequency can lead to the development of recalcitrant understory layers. Mallik (2003) hypothesized that long-term fire suppression in logged or defoliated stands led to forest “conversion” to *Kalmia*, *Calluna*, and *Gaultheria* heathlands. In temperate forest systems, fire suppression and canopy disturbances contribute to the spread of rhododendron and mountain laurel (*Kalmia latifolia*). These species now form recalcitrant understory layers that cover an estimated 2.5 million hectares in the southeastern U.S. alone (Table 2.2; Monk et al. 1985, Vandermast and Van Lear 2002).

The separate and combined effects of disturbances and browsing act as a strong filters on species richness creating depauperate understories dominated by one or a few species. Overbrowsing selects for only those species that are well defended or tolerant to browsing (e.g. Horsley et al. 2003, Banta et al. 2005). Frequent fires select for only those species that can survive the fire or resprout thereafter (e.g. Gliessman 1978, Mallik 2003, Payette and Delwaide 2003). Finally, increased overstory disturbance selects for shade-intolerant species with rapid rates of vegetative spread vs. slower growing shade-tolerant herbs and shrubs (e.g. Ehrenfeld 1980, Moola and Mallik 1998, Schnitzer et al. 2000). Ultimately, these processes create novel conditions that favor only a small subset of species that typically spread vegetatively, are fast-growing, relatively shade-intolerant, fire-tolerant, and herbivore-tolerant (Table 2.1). The result is a low diversity but dense understory that can persist for long periods of time even if the canopy closes.

#### **2.3.4 Summary**

We found that major anthropogenic changes to disturbance and browsing regimes underlie the development of most recalcitrant understory layers. Indeed, overbrowsing, altered fire regimes, and increased overstory disturbance were implicated in 18, 34, and 82% of the cases, respectively (Table 2.1). More importantly, our review suggests that the formation of a dense understory canopy layer often arises (53%) when overstory disturbances and altered understory fire and browsing regimes occur in tandem (Table 2.1). Additionally, these understory layers are depauperate because repeated canopy disturbances combined with other processes (i.e., fire and browsing) strongly favor a small subset of species.

### **2.4 RECALCITRANT UNDERSTORY LAYERS ARREST, DELAY, AND ALTER FOREST SUCCESSION**

#### **2.4.1 Arrested Succession**

In a small number of documented cases, recalcitrant understory layers appear to exclude tree regeneration for extended periods of time. This pathway is described by a variety of terms including ‘self-perpetuating climax community’ (Horsley and Marquis 1983), ‘alternate stable state’ (Schmitz and Sinclair 1997, Stromayer and Warren 1997), ‘polyclimax’ (Tansley 1935), or ‘arrested succession’ (Niering and Goodwin 1974). Although the long-term stability of these systems is difficult to confirm (Sutherland 1974, Connell and Sousa 1983, Peterson 1984, Sutherland 1990), there are compelling examples where shrubs and ferns have persisted for decades in stands formerly dominated by trees (Niering and Egler 1955, Horsley 1985, Koop and Hilgen 1987, Raich and Christensen 1989, Petraitis and Latham 1999, Den Ouden 2000, Latham 2003, Mallik 2003). It is unclear whether these layers are self-sustaining (e.g., via strong



interference) or if continued browsing or frequent fire is required to perpetuate them and retard the reestablishment of trees (Hill 1996, Mallik 2003).

#### **2.4.2 Delayed Succession**

A recalcitrant understory layer can slow the *growth rate* of tree species thereby slowing the rate of successional change without altering the eventual tree species composition. For example, in boreal forests, the grass *Calamagrostis canadensis* suppresses the regeneration of dominant tree species, including white spruce (*Picea glauca*). This delays stand development by 20 – 30 years until saplings eventually emerge through the *C. canadensis* canopy and the stands revert to forest (reviewed by Lieffers et al. 1993). Delayed successions also occur in other boreal forests where a dense ericaceous shrub layer suppresses the growth and emergence of tree species including western red cedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and Norway spruce (*Picea abies*) (Messier et al. 1989, Messier and Kimmins 1991, Mallik 1995, Maubon et al. 1995).

Additionally, a recalcitrant understory layer may reduce tree species *survivorship* sufficiently to delay gap-phase succession. For example, in tropical forests, gaps promote the expansion of resident understory lianas (Schnitzer et al. 2000). These understory lianas can become so dense after gap creation that they inhibit the subsequent growth and survival of both pioneers and shade-tolerant trees, thus stalling succession for decades (Schnitzer et al. 2000). This dynamic of delayed gap-phase regeneration occurs in tropical and temperate forests where lianas, fern, and bamboo thickets effectively clog gaps (Kochummen and Ng 1977, Taylor and Zisheng 1988, Guariguata 1990, Walker 1994, Schnitzer et al. 2000, Abe et al. 2002). In time, trees emerge from this layer and reach the canopy apparently with little impact on community diversity (Abe et al. 2002).

### **2.4.3 Altered Gap-Phase Regeneration**

A recalcitrant understory layer may differentially reduce establishment among co-occurring tree species, thereby controlling the composition of the advance regeneration layer (George and Bazzaz 1999a,b). Dense understories create conditions near the soil surface that are inimical to tree germination and early growth and survivorship. For example, understory layers that generate a thick litter layer may inhibit germination of small-seeded species (George and Bazzaz 1999a, Farris-Lopez et al. 2004) while those that strongly preempt light can preclude the establishment of any but the most shade-tolerant species (Horsley 1993a, de la Cretaz and Kelty 2002, Gonzalez et al. 2002). These dense layers may substantially suppress tree recruitment by a combination of at least six different types of interference mechanisms (Table 2.1). Consequently, only a few tree species may possess the necessary traits to persist under and eventually emerge thru this understory layer to constitute the advance regeneration layer (Runkle 1990, Connell 1990). If so, then the species composition of the advance regeneration layer and subsequent pattern of gap-phase dynamics will contrast sharply in forests with a recalcitrant understory layer vs. one without.

## **2.5 MECHANISMS OF INTERFERENCE OVER TREE ESTABLISHMENT, SURVIVAL, AND GROWTH**

A dense understory canopy can suppress regeneration directly via resource competition, allelopathy, creating a barrier for seed germination, and physical damage or indirectly through modifications of interspecific interactions (Figure 2.2). Because most studies fail to distinguish among these mechanisms, Muller (1969) proposed the term interference to describe the suppression of one species or layer on another species. Below, we briefly review the literature to evaluate the evidence for six different mechanisms of interference between the understory layer

and co-occurring tree species. We suggest that the most efficient and cost effective remediation of the deleterious effects of these recalcitrant understory layers will require a greater understanding of how these layers alter patterns of forest regeneration and succession (see below)

### **2.5.1 Resource Competition.**

In closed canopy forests, dense understories exacerbate the degree of light attenuation caused by the midstory and canopy (Messier et al. 1998, Beckage et al. 2000, Nilsen et al. 2001, de la Cretaz and Kelty 2002). Photosynthetically active radiation (PAR) levels can drop well below 5% of of full sun beneath these layers (Nakashizuka 1987, Kelly and Canham 1992, Horsley 1993a, Wada 1993, Walker 1994, Clinton and Vose 1996, Hill 1996, George and Bazzaz 1999a, Aubin et al. 2000, Lusk 2001, Lei et al. 2002). Additionally, these dense low canopies can reduce light quality, (e.g., red:far-red wavelengths) thereby preventing germination, altering internode elongation, and inhibiting flowering (Messier et al. 1989, Horsley 1993a, Mancinelli 1994). Furthermore, dense low canopies decrease the availability of sunflecks particularly for seedlings (Denslow et al. 1991, Nilsen et al. 2001, Lei et al. 2002). Finally, if canopy gaps do form, they may not operate as gaps at all if seedlings remain trapped beneath a dense understory layer (Beckage et al. 2000, Lusk 2001). Under this scenario, regeneration may be limited to only a few individuals of those few species that are highly shade-tolerant.

Dense understories may also exacerbate belowground competition (Putz and Canham 1992, Messier 1993, Dillenburgh et al. 1993). Some studies infer resource limitation by detecting increased growth or survival of target plants following fertilization or measuring lower nutrient and water concentrations in soil beneath dense understory cover vs. more open areas (e.g. Messier 1993, Yamasaki et al. 1998, Inderjit and Mallik 1996, Nilsen et al. 2001).

Similarly, vine-covered saplings often have lower foliar nitrogen levels, reduced pre-leaf water potential, and decreased diameter growth when compared to vine-free saplings (Dillenburgh et al. 1993, Perez-Salicrup and Barker 2000). The above studies are suggestive of resource limitation though they typically do not distinguish between competition for water vs. soil nutrients. Because nutrient and water availability covary, decoupling these two factors is difficult (Nambiar and Sands 1993, Casper and Jackson 1997). Additionally, few experiments use factorial manipulations to disentangle a dense understory layer's above- vs. belowground effects and their interactions (McPhee and Aarssen 2001).

Horsley (1993a) experimentally tested the influence of above vs. below ground competition. He tied back hay-scented fern fronds while leaving their roots and rhizomes intact thereby reducing light competition and isolated seedlings within PVC tubes thereby reducing root competition. He found that light attenuation, and not belowground competition, was the mechanism of interference (Horsley 1977, Horsley 1993a, Horsley 1993b). Putz and Canham (1992) conducted similar above- and belowground manipulations. They found that a dense understory layer reduced tree regeneration primarily because of below-ground competition (see also Christy 1986) although this varied with soil fertility. Belowground competition was more important in infertile sites whereas aboveground competition was more important in fertile sites. Clearly well-replicated factorial experiments are required to ascertain the relative importance of below- and aboveground competition though these studies may ignore other processes that may confound the results of these experiments (e.g., allelopathy, see below).

### **2.5.2 Allelopathy**

Direct field evidence for allelopathy remains equivocal and elusive. In forests that have dense understories dominated by ericaceous shrubs, phenolics and other phytochemical compounds can

disrupt nitrogen mineralization and inhibit ectomycorrhizal fungi; this significantly reduces conifer growth and survivorship (Walker et al. 1999; reviewed by Mallik 1995, 2003 and Wardle et al. 1998). In these systems, Nilsson (1994) used factorial manipulations of above and below-ground competition and allelopathy to identify how the boreal shrub *Empetrum hermaphroditum* suppressed tree regeneration. She found that both below-ground competition and allelopathy were important but that belowground competition played the primary role. Similarly, Jäderlund et al. (1997) found that *Vaccinium myrtillus* interfered with Norway Spruce (*Picea abies*) primarily through belowground competition. In forests where ferns form dense understories, bioassays and greenhouse studies have suggested the potential for strong allelopathic effects on tree regeneration (Gliessman and Muller 1972, Horsley 1977, Gliessman and Muller 1978); however, further field experimentation failed to find strong allelopathic effects (Horsley 1993b, Dolling 1996, Nilsen et al. 1999, den Ouden 2000). Despite these results, too few studies have tried to experimentally disentangle resource competition from allelopathy via field experiments. Future research must move beyond merely documenting the mere existence of phytotoxic exudates in greenhouse and laboratory studies (Fuerst and Putnam 1983, Williamson 1990, Weidenhamer 1996, Inderjit and Callaway 2003).

### **2.5.3 Apparent Competition**

A dense understory layer can increase the activity of small mammals thereby increasing the rate and impact of seed and seedling predation (Gliessman 1978, Wada 1993, George and Bazzaz 1999, Den Ouden 2000, Schreiner et al. 2000). This can create a situation where it appears that low seedling densities are caused by resource competition (e.g., light attenuation) when in fact they are caused by predation (Holt 1977, 1984, Connell 1990). Connell (1990) defined this as a type of Apparent Competition (*sensu* Holt 1977, 1984). Experiments that use canopy removals

confound the direct competitive release of removing the understory layer with the indirect effects of removing this layer, particularly decreasing small mammal predation (Reader 1993). Even though small mammals are abundant, forage preferentially beneath dense vegetative cover, and consume copious quantities of seeds, few experiments have attempted to evaluate Apparent Competition vs. resource competition. Nonetheless, long-term studies in other plant systems have documented that selective seed and seedling predation can lead to rapid changes in plant community composition (e.g. Brown and Heske 1990, Ostfeld and Canham 1993, Howe and Brown 2001).

#### **2.5.4 Litter Accumulation**

A thick litter layer typically reduces plant species diversity and density through a wide variety of direct and indirect mechanisms (see Facelli and Pickett 1991). For example, George and Bazzaz (1999a) found that a thick fern litter layer directly limited the establishment of small-seeded tree species (see also Veblen 1982, Beckage et al. 2000, Lei et al. 2002, and Farris-Lopez et al. 2004). Alternatively, in boreal forests, the insulative properties of a dense grass litter layer results in decreased soil nitrogen mineralization, water uptake, and seedling photosynthetic rates, thus indirectly diminishing conifer growth and survival (Hogg and Lieffers 1991, Lieffers et al. 1993, Cater and Chapin 2000). Aside from these examples, there are few experimental tests that unravel the many facets of litter interference or evaluate its importance relative to other mechanisms (e.g. resource competition). However, in forests characterized by a recalcitrant understory litter layer, it is clear that this alternative remains a viable and potentially important mechanism.

### **2.5.5 Mechanical Interference**

A dense understory layer can reduce tree seedling regeneration via non-competitive, physical interference. Clark and Clark (1991) demonstrated that the passive shedding of branches and leaves of subcanopy palms smothered seedlings present in the understory. Similarly, collapsing *Guadua* bamboo culms can reduce tree seedling growth and survival (Griscom and Ashton 2003). Additionally, the physical weight of a large liana load may suppress tree seedling and sapling growth (Putz 1991, Gerwing 2001, Schnitzer et al. 2004). If tree species respond differentially to these physical stresses, then this mechanism alone can potentially alter understory tree species composition and modify future successional trajectories (e.g. Guarigauta 1998, Gillman et al. 2003).

### **2.5.6 The relationship between mechanisms of interference and phenology**

The intensity and duration of any particular interference mechanism can vary temporally as a result of the species' life-history, whether evergreen, deciduous, or monocarpic. In fact, this trait may provide clues to understand both the strength and type of interference. For example, evergreen species may pose a greater impediment to tree regeneration as their effects are exerted throughout the year on all tree seedling life-history transitions (Givnish 2002). In contrast, herbaceous perennials that senesce in the fall or deciduous shrubby species only exert competitive effects during the growing season (e.g. Nilsen et al. 2001, de la Cretaz and Kelty 2002). This delayed expansion of the recalcitrant understory layer provides a brief window of opportunity for evergreen tree species, species with early germination (e.g. *Acer rubrum*), or species with early leaf expansion (e.g. *Betula lenta*) to overcome the understory stratum's deleterious effects on early establishment. This temporal advantage can provide sufficient photosynthetic and growth opportunity for tree species to adopt a 'sit and wait' strategy (de la

Cretaz and Kelty 2002). Additionally, if the intensity of apparent competition decreases with senescence of the low canopy, then the impact of pervasive seed predation may decrease in the fall. This timing of senescence may generate increased predation on early seed dispersers (e.g., *Quercus* spp.) relative to later dispersers (e.g., *Acer saccharum*, *Fagus grandifolia*).

## **2.6 ON THE CAUSES AND CONSEQUENCES OF A RECALCITRANT UNDERSTORY LAYER**

We contend that the expansion and monopolization of the understory by a narrow set of plant species is often an inadvertent outcome of policies and management decisions that deviate from natural forest overstory disturbance, fire, and herbivory regimes. We propose a general conceptual model through which alterations in the dynamics of the overstory, understory, or both generate increases in a select few understory plant species (Figure 2.1). These alterations involve changes in the frequency and scale of overstory disturbance, increased or decreased fire frequency, or increased herbivory that release a restricted set of understory species from prior competitive constraints. Once released, these species increase dramatically in abundance and cover over large portions of the forested landscape (Table 2.1). Following its establishment, this recalcitrant understory layer interferes with tree regeneration through a variety of direct and indirect mechanisms including above- and belowground competition, allelopathy, apparent competition, litter, and mechanical damage. Consequently, this recalcitrant layer itself inhibits tree regeneration and strongly influences which tree species establish and survive beneath its canopy (e.g. Veblen 1982, Clinton et al. 1994, Dolling 1996, Cater and Chapin 2000). The strength and selectivity of this filter can retard succession, alter the tree species participating in the successional sere, or potentially arrest succession.

We found only 25% of the published studies reviewed reported results of manipulative field experiments designed to identify the existence of  $\geq 1$  particular interference mechanism(s)



(Table 2.1). Above- and belowground competition and allelopathy were the predominant mechanisms tested, 37, 32, and 13%, respectively (Table 2.1). Apart from competition and allelopathy, many papers speculated on various interference mechanisms but few, if any, were tested experimentally. Given the paucity of information, it is clear that for most systems, we lack the information to clearly establish by which mechanism a recalcitrant understory layer inhibits tree regeneration (see Levine et al. 2003 for similar conclusion on exotic invasives).

We argue that to move towards a more mechanistic understanding of the ‘interference’ phenomenon could begin by considering the most limiting resource(s) within a given system. For example, on a coarse scale, forested ecosystems differ in the identity of the most limiting resource(s) [e.g. light, soil nutrients, and water] and these differences could provide insight into the most plausible interference mechanism. Boreal and cool-temperate forests are typically nutrient poor (primarily N) and less light limited relative to their temperate and tropical counterparts (Krause et al. 1978, Attiwill and Adams 1993, Kimmins 1996, Reich et al. 1997, reviewed by Coomes and Grubb 2000, Ricard et al. 2003). We found that dense low canopies in these forest types suppress regeneration directly via belowground competition and indirectly via allelopathic interactions that mediate resource availability and uptake (Table 2.1; Christy 1986, Nilsson 1994, Jäderlund et al. 1997). In contrast, temperate deciduous and tropical rainforests tend to be light limited (Pacala et al. 1994, Finzi and Canham 2000). In these systems, we found that other mechanisms including aboveground competition and seed predation were generally more important than belowground competition (Table 2.1; Denslow et al. 1991, Horsley 1993a, den Ouden 2000). Ideally, the best tests would link a series of carefully controlled laboratory or greenhouse studies with field experimentation in order to identify which mechanisms merit further investigation. Furthermore, we strongly argue that factorial experiments remain the best

experimental design to test the relative importance of each factor independently as well as any interactions.

## **2.7 IMPLICATIONS FOR FLORISTIC DIVERSITY AND FOREST SUCCESSION**

The increasingly common development of recalcitrant understory layers worldwide plays a strong, yet vastly underestimated, role in determining future successional patterns, forest composition and diversity because of their tendency to selectively suppress tree regeneration. Indeed, studies examining the regeneration success of a variety of tree species demonstrate that a majority of tree species suffer decreased seedling densities and limited height growth underneath recalcitrant understory canopies (e.g. Horsley and Marquis 1983, George and Bazazz 1999a,b, de la Cretaz and Kelty 2002, Hille Ris Lambers and Clark 2003). The presence of this additional filter on floristic diversity in forest understories together with increased herbivory and altered fire regimes undoubtedly restricts the number of species that can successfully regenerate. The potential consequences of these ecological filters (*sensu* George and Bazazz 1999) on species composition remains poorly understood. Nevertheless, we suggest that floristic diversity in such areas is so severely constricted that succession may steadily march toward monodominance or complete regeneration failure. These extreme cases include the fern and grass covered ‘orchard’ stands in Pennsylvania where 50 – 80 year old failed clear-cuts remain devoid of tree regeneration (Horsley 1985) or bracken covered tropical regions of Central America that have persisted for centuries following forest removal (den Ouden 2000).

### **2.7.1 Forest Dynamics Models**

Computer-based forest successional models (e.g. JABOWA-FORET [Shugart and West 1977, Smith and Urban 1988] and SORTIE [Pacala et al. 1996]) remain the best tool to explore long-term successional outcomes; however, forest dynamics models typically fail to include a dense

understory layer's impact on early seedling survival and growth. For example, in SORTIE, the growth and mortality parameters are derived from saplings (15 – 750 cm in height) are applied seedlings as well (Pacala et al. 1994, Kobe et al. 1995). Furthermore, although the recruitment parameter for most species in SORTIE is fit using distributions of first-year seedlings (Ribbens et al. 1994) their survivorship is assumed to be 100% until age five, the age at which individuals enter the model (Pacala et al. 1996). The authors acknowledge their recruitment parameter estimate is potentially unreliable as the survival of individuals < 5 years old is highly variable and mortality is often intense (Pacala et al. 1996). Indeed, researchers have documented that density dependent (e.g. Packer and Clay 2000) and density independent mortality can dramatically alter initial seedling distribution patterns, particularly under a dense understory layer (Hille Ris Lambers and Clark 2003, Schnurr et al. 2004). By constraining the model and its parameters to the  $\geq 5$  year old age class SORTIE assumes away all the early dynamics that may occur low to the ground underneath a recalcitrant understory layer and help shape the composition sapling class.

We know of only one effort to integrate a recalcitrant understory layer into SORTIE. Hill (1996) incorporated hay-scented fern abundance as a function of light as well as hay-scented fern's impact on light availability as a function of frond density. With the increased light limitation imposed by fern cover, successional projections indicated faster reductions in shade intolerant species abundance and an accelerated shift towards dominance by shade tolerant species (Hill 1996). Nevertheless, all simulations containing a dense fern layer did not mirror complete regeneration failure documented in the field (Hill 1996). We concur with Hill that the inconsistencies between model projections and observable field patterns likely result from overestimates in seedling growth and an underestimates in seedling mortality inherent in

SORTIE. We argue these inconsistencies are due to 1) ignoring the early (< 5 years) seedling dynamics and 2) a failure to incorporate additional interference mechanisms causing seedling mortality (e.g. apparent competition) beyond light competition.

### **2.7.2 Forest Management**

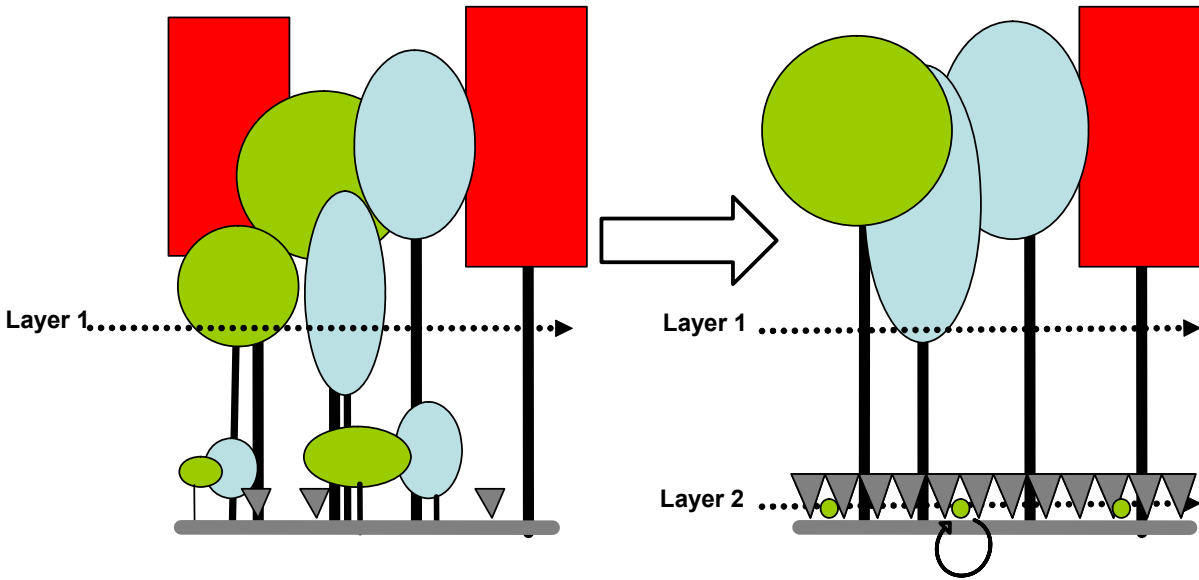
The framework advanced by this review could aid land managers in implementing informed management policies and practices that both limit the spread of these plants and target control and remediation treatments directed at the precise mechanism of interference. We found that alterations forest canopy disturbance, fire, and herbivory regimes may lead to the establishment of recalcitrant understory layers, particularly when alterations to the overstory and understory disturbance regimes occur in tandem (e.g. Payette and Delwaide 2003). We suggest managers monitor overstory and understory conditions to ensure that modifications to either of these strata do not operate concurrently in an effort to mitigate invasion risk. Furthermore, care should be taken when the control over overstory and understory factors fall under the purview of different agencies (e.g. wild game vs. forestry management agencies). We caution that decisions regarding partial or complete overstory removals should consider the site's understory conditions including inadequate advance regeneration, presence of clonal understory plants, and high herbivore impact (e.g. Marquis et al. 1990). Finally, we further suggest the implementation of management practices that more closely resemble natural disturbance levels.

Understanding the interfering plant species' ecology could provide managers with alternative treatments to promote tree regeneration when conventional treatments like herbicide are not desired or permitted (Berkowitz et al. 1995). For example, mowing or cutting of ferns, grasses, and shrubby interfering vegetation may successfully ameliorate their aboveground competitive effects and enhance regeneration (Davies 1985, Marrs et al. 1998, Biring et al.

2003). Alternatively, if belowground competition is the major interference mechanism, fertilizer application may mitigate the competitive effects of interfering plants and promote tree regeneration (Prescott et al. 1993, Haywood et al. 2003). Additional remediation techniques tailored to other interference mechanisms could include direct seeding of propagules coated with small mammal repellent (Campbell 1981, Nolte and Barnett 2000), soil scarification or controlled burning to reduce litter interference (Nyland 2002), and activated carbon as a treatment to mitigate allelopathic interference (Jäderlund et al. 1998). Finally, a basic understanding of possible successional outcomes following the establishment of a low canopy may aid land managers. In areas where the low canopy simply stalls succession, successful regeneration will ultimately occur without any silvicultural techniques. Finally, where the recalcitrant understory layer filters tree species composition or arrests succession, managers could manipulate the rate and direction of regeneration by underplanting tree species relatively unaffected by the interfering layer (e.g., shade tolerant species) in order to attain a desirable and diverse mix regeneration outcome (Löf 2000).

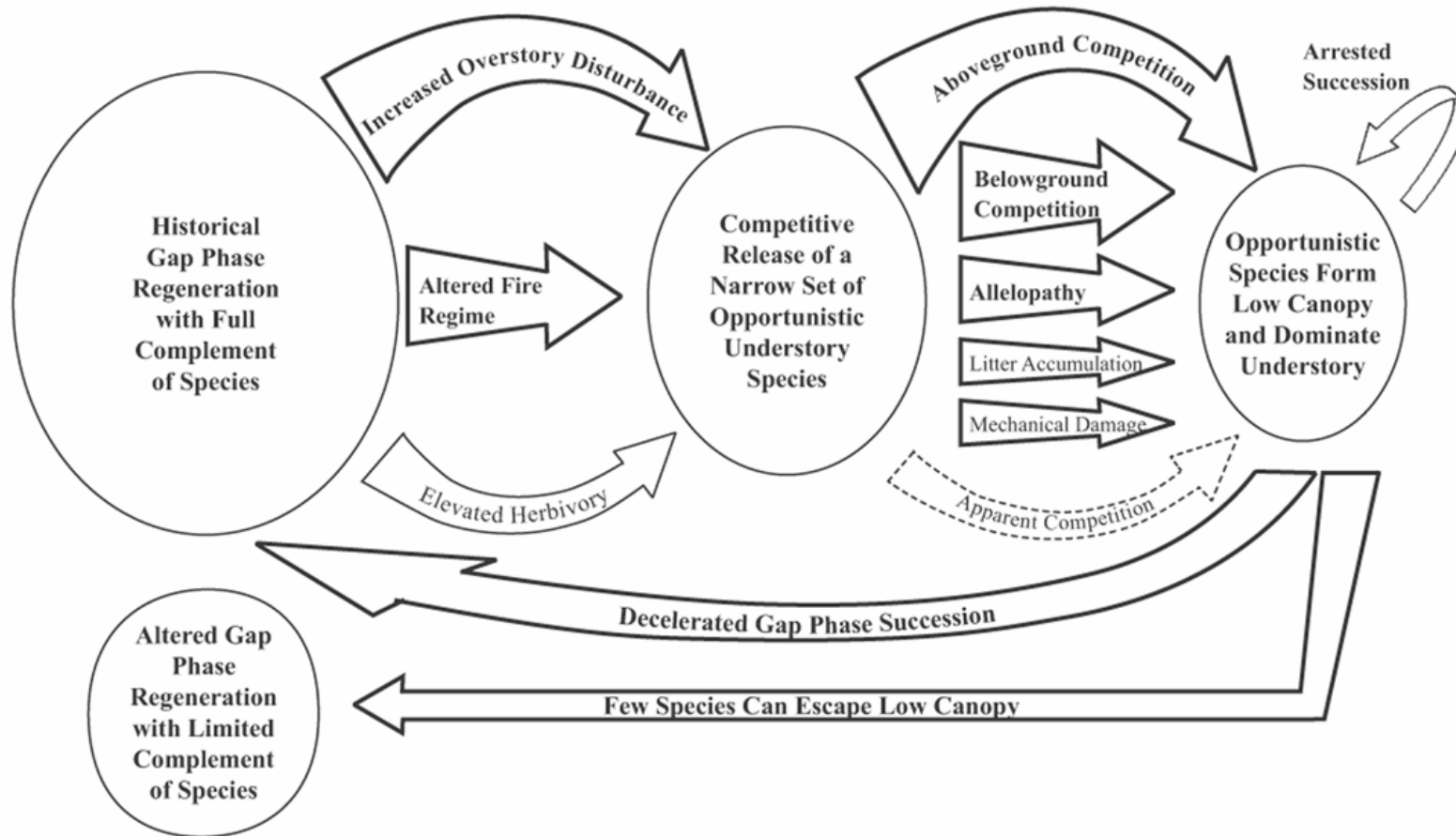
## Figure 2.1 Recalcitrant Understory Layer Formation.

Diagrammatic representation of the conversion from A) forests containing a diverse and structured advanced regeneration layer with sparse understory plant abundance (▼) to B) forests where a native understory species expands and monopolizes the understory. The dense herbaceous or shrubby cover represents a new vegetation layer that exerts direct and indirect interference effects and prevents seedling (●) recruitment into the sapling class. C) Example with hay-scented fern in northwestern Pennsylvania forests.



**Figure 2.2 Causes and consequences of recalcitrant understory layer.**

Conceptual model illustrating factors precipitating change from historical gap-phase regeneration into low canopy dominance. The model also reveals various interference mechanisms and illustrates the ensuing successional pathways. The size of the arrows denotes the relative importance of each transition as revealed by our review.



**Table 2.1 Occurrence of dense, monodominant understory species.**

Summary of whether the species possess rapid vegetative growth, if their increase in abundance is linked to alterations in the herbivory, fire, or overstory disturbance regimes, and whether they are fire or browse tolerant (T). “Mechanism” indicates the specific interference mechanisms exerted by a species (1 = aboveground competition, 2 = belowground competition, 3 = allelopathy, 4 = apparent competition, 5 = litter, and 6 = mechanical damage). Mechanisms in bold were tested using manipulative field experiments and those in brackets are speculative.

Species	Family	Areas Affected	Rapid Vegetative Growth	Herbivory	Fire	Overstory Disturbance	Mechanism	References
<i>Dennstaedtia punctilobula</i>	Dennstaedtiaceae	NE US	√	√ (T)	-	√	<b>1,2,3,5 [4]</b>	Cody et al. 1977; Anderson and Egler 1988; Drew 1988, 1990; McWilliams et al. 1995; de la Cretaz & Kelly 1999, 2002; George & Bazazz 1999 a,b; Horsley & Marquis 1983; Horsley 1977, 1993 a,b; Horsley et al. 2003; Hill 1996; Hill & Silander 2001; Brach et al. 1993
<i>Pteridium aquilinum</i>	Dennstaedtiaceae	Worldwide	√	-	√ (T)	√	<b>1,2,3,5 [4]</b>	Gleissman 1972, 1978, Gleissman & Muller 1978; Dolling 1996, 1999; Dolling et al. 1994; Ferguson and Adams 1994; den Ouden 2000
<i>Thelypteris novaborensis</i>	Thelypteridaceae	NE US	√	√ (T)	-	√	<b>[1]</b>	Hill & Silander 2001
<i>Blechnum</i> spp.	Blechnaceae	New Zealand	√	√ (T)	-	√	-	Cunningham 1979; Coomes et al. 2003
<i>Cyathea</i> spp.,	Cyatheaceae	New Zealand	√	√ (T)	-	√	-	Jane & Pracy 1974; Rogers & Leathwick 1997
<i>Dicranopteris linearis</i>	Gleicheniaceae	Sri Lanka, Hawaii	√	-	√	√	-	Maheswaran & Gunatilleke 1988, Russell et al. 1998
<i>Dicranopteris pectinata</i>	Gleicheniaceae	Puerto Rico	√	-	√	√	<b>[1]</b>	Guariguata 1990; Walker 1994; Walker & Boneta 1995; Russell et al. 1998; May 2000
<i>Gleichenia bifida</i>	Gleicheniaceae	Puerto Rico	√	-	√	√	-	Guariguata 1990; Walker and Boneta 1995
<i>Gleichenia linearis</i>	Gleicheniaceae	Malasia	√	-		√	-	Kochummen & Ng 1977
<i>Calamagrostis canadense</i>	Gramineae	N. America Boreal Forests	√	-	√ (T)	√	<b>1,5 [4]</b>	Hogg & Lieffers 1991; Lieffers et al. 1993; Cater & Chapin 2000
<i>Cortaderia</i> spp.	Gramineae	New Zealand	√	√	-	√	-	Jane & Pracy 1974; Rogers & Leathwick 1997
<i>Deschampsia flexuosa</i>	Poaceae	European Boreal Forests	√	√ (T)	-	√	-	Berquist et al. 1999
<i>Astogyne martiana</i>	Arecaceae	Costa Rica	-	-	-	-	<b>1,2,[7]</b>	Denslow et al. 1991
<i>Geonoma cuneata</i>	Arecaceae	Costa Rica	-	-	-	-	<b>1,2,[7]</b>	Denslow et al. 1991
<i>Oenocarpus mapora</i>	Arecaceae	Costa Rica	√	-	-	-	<b>6,[1]</b>	Farris-Lopez et al. 2004
<i>Asplundia uncinata</i>	Cyclanthaceae	Costa Rica		-	-	-	<b>1,2,[7]</b>	Denslow et al. 1991
<i>Aechmea magdalenae</i>	Bromeliaceae	Panama	√	-	-	√	<b>[1]</b>	Brokaw 1983, Pfitsch & Smith 1988
<i>Sinarundinaria gangiana</i>	Poaceae	China	√	-	-	-	-	Taylor & Zisheng 1988
<i>Chusquea</i> spp.	Poaceae	W. South America	√	-	-	√	<b>[1,4]</b>	Veblen 1982; Lusk 2001; Gonzalez et al. 2002



Table 2.1 (cont.)

Species	Family	Areas Affected	Rapid Vegetative Growth	Herbivory	Fire	Overstory Disturbance	Mechanism	References
<i>Guadua sarcocarpa</i>	Poaceae	S. America	√	-	√	√	[1,6]	Griscom & Ashton 2003
<i>Fargesia denudata</i>	Poaceae	China	√	-	-	-	-	Taylor et al. 1995
<i>Sasa spp.</i>	Poaceae	Japan	√	-	-	√	[1,4]	Wada 1993; Abe et al. 2002; Iida 2004
<i>Yushania microphylla</i>	Poaceae	Bhutan	√	-	-	-	[1]	Gratzer et al. 1999
<i>Calluna vulgaris</i>	Ericaceae	W. Europe	√	-	√ (T)	√	[3]	Mallik 1995
<i>Kalmia angustifolia</i>	Ericaceae	Eastern Canada & US	√	-	√ (T)	√	[2,3]	Hall et al. 1973; Meades 1983; Mallik 1995; Inderjit & Mallik 1996; Mallik & Inderjit 2001; Bradley 1997; Yamasaki et al. 1998
<i>Kalmia latifolia</i>	Ericaceae	Eastern USA	√	-	√ (T)	√	[1]	Woods & Shanks 1959; Monk et al. 1985; Lipscomb and Nilsen 1990; Mallik 1995
<i>Rhododendron maximum</i>	Ericaceae	Eastern U.S.	√	-	√ (T)	√	1,[2,3,4,5]	Monk et al. 1985; Lipscomb and Nilsen 1990; Clinton et al. 1994; Clinton & Vose 1996; Walker et al. 1999; Nilsen et al. 1999, 2001; Beckage et al. 2000; Lei et al. 2002; Vandermaast et al. 2002; Beckage & Clark 2003; Christy 1986; Hille Ris Lambers & Clark 2003; Vandermaast & Van Lear 2002
<i>Gaylussaccia baccata</i>	Ericaceae	Eastern U.S.	√	-	-	√	1,2	Beckage and Clark 2003
<i>Gaultheria shallon</i>	Ericaceae	W. Canada Pacific NW	√	-	√ (T)	√	3	Price et al. 1986; Messier and Kimmins 1990, 1991; Klinka 1989; Messier 1992, 1993; Chang & Preston 2000; Chang et al. 1996a,b; Bunnell 1990
<i>Vaccinium myrtillus</i>	Ericaceae	European Boreal Forests	√	-	√ (T)	√	1,2,3	Maubon 1995; Jäderlund et al. 1997; Moola & Mallik 1998; Frak & Ponge 2002
<i>Empetrum hermaphroditum</i>	Ericaceae	European Boreal Forests	√	-	-	√	1,2,3	Michelsen et al. 1995; Mallik 2003; Nilsson 1994; Wardle and Nilsson 1997; Zackrisson et al. 1997; Nilsson et al. 2000
<i>Pseudowintera colorata</i>	Winteraceae	New Zealand	-	√ (T)	-	√	-	Godley & Smith 1981; Allen et al. 1984; Coomes et al. 2003; Husheer et al. 2003
<i>Rubus spp.</i>	Rosaceae	Pacific NW & Europe	√	-	-	√	[1,4,5]	Franklin and Pechanec 1967; Tappener et al. 1991; Schreiner et al. 2000
<i>Rhus glabra</i>	Anacardiaceae	Eastern USA	√	-	-	√	1,2	Putz & Canham 1992
Lianas (various genera)	-	Tropical Forests & Eastern US	√	-	√	√	1,2,[6]	Smith 1984; Dillenberg et al. 1993; Perez-Salicrup & Barker 2000; Schnitzer et al. 2000; Schnitzer & Bongers 2002; Gerwing 2001; Grauel & Putz 2004
<i>Cornus spp.</i>	Cornaceae	NE US	√	-	-	√	1,2	Ehrenfeld 1980; Huenneke 1983; Putz & Canham 1992
<i>Corylus cornuta</i>	Betulaceae	Lake States US	√	-	-	√	1,2	Sabhasri and Williams 1960; Batzer and Popp 1985; Tappener 1971; Tappeiner & John 1973; Tappeiner et al. 1991, 2001; Kurmis and Sucoff 1989
<i>Acer spicatum</i>	Aceraceae	SE Canada, NE US	√	-	-	√	[1]	Aubin et al. 2000

**Table 2.2 Estimates spatial coverage by recalcitrant understory layers.**

Coverage data convey either the total forested land area (in hectares) or the proportion of forested area dominated by a particular species within a region.

Species	Location	Forest Type	Estimated Area Affected (ha)	Proportion of Forested Area Affected	References
<i>Dennstaedtia punctilobula</i>	Pennsylvania	Temperate Hardwoods	2.1 million	0.33	McWilliams, et al. 1995
<i>Dennstaedtia punctilobula</i>	Allegheny National Forest, Pennsylvania	Temperate Hardwoods	52,000 - 72,000	~0.35	Royo, unpub. data
<i>Rhododendron maximum</i>	Southern Appalachian Region, U.S.	Temperate Hardwoods	2.5 million	-	Monk et al. 1985
<i>Sasa spp.</i>	Japan	Temperate Hardwoods	6.9 million	0.25	Kobe 1984
Lianas (various genera)	Barro Colorado, Rep. Of Panama	Tropical Forests	-	~0.22 of all gaps	Schnitzer et al. 2000
<i>Pteridium aquilinum</i>	Fontainebleau Forest, France	Old Growth Beech Forest	-	.02 - .17	Koop and Hilgen 1987
<i>Pteridium aquilinum</i>	The Netherlands	Temperate Hardwood and Conifer	288,500	~0.7 of entire country	den Ouden 2000
<i>Kalmia angustifolia</i>	Newfoundland, Canada	Black Spruce	-	0.55	English and Hackett 1994 (cited in mallik 2001)
<i>Gaultheria shallon</i>	British Columbia	cedar/hemlock forest	100,000	-	Wheetman et al. 1990
<i>Guadua sarcocarpa</i>	Amazonia	Tropical Forests	18 million	-	Nelson 1994
<i>Calamagrostis canadensis</i>	Western Canadian Provinces	Boreal Forests	-	0.25 - 0.5 of all cutover forest	Lieffers, pers comm.

### **3.0 DIRECT AND INDIRECT EFFECTS OF HAY-SCENTED FERN ON TREE SEEDLINGS: A CASE FOR APPARENT COMPETITION**

#### **3.1 ABSTRACT**

An extension of the classic apparent competition model posits that one plant species can provide a favorable microhabitat for herbivores, thereby indirectly reducing densities of a second vulnerable species via increased predation. In forest understories dominated by dense herbaceous or shrubby layers, this model provides a viable and compelling alternative to competition in explaining how these understory layers reduce tree seedling recruitment and thus alter patterns of forest regeneration. We tested this model in northern hardwood forests in Pennsylvania with dense understories of hay-scented fern (*Dennstaedtia punctilobula*). The apparent competition hypothesis predicts that seedling establishment should be lower in fern covered areas with small mammals present vs. those devoid of small mammals. To test this hypothesis we manipulated fern cover and the presence and absence of small mammals in a factorial design. In support of our hypothesis, we found that mammalian activity was greater beneath fern cover. Seed removal trials revealed clear preferences by rodents in the absence of fern cover. Fern cover exerted an indirect apparent competitive effect by decreasing black cherry (*Prunus serotina*) emergence. Furthermore, fern cover exerted a direct competitive effect on black cherry and red maple (*Acer rubrum*) survival as well as on red maple germination. This is one of a few tests of the apparent competition model in plant communities and our results demonstrate that microhabitat influenced predation strongly limits seedling establishment. Thus,

elucidating the role of small mammals is critical since it could force us to reevaluate our understanding of the factors controlling forest development.

### **3.2 INTRODUCTION**

In many forested areas worldwide, native understory herbs and shrubs often form region-wide dense clonal patches that suppress seedling density and inhibit tree species recruitment into the sapling stage (Royo & Carson, in review). Because this dense understory layer is only a few meters tall, it represents one of the first filters structuring seedling layer recruitment and composition (George and Bazzaz 1999a,b). Indeed, both Runkle (1990) and Connell (1997) hypothesized that the composition of the advance regeneration layer and subsequent successional trajectories may hinge interactions between the understory layer and tree seedling recruitment (see also George and Bazzaz 1999, Lusk 2001). Nonetheless, gap dynamics theory and forest simulation models typically ignore events occurring prior to gap formation and assume that understory herbs and shrubs have little impact on the seedling layer composition.

Most studies investigating how a dense understory layer inhibits regeneration are focused on this dense stratum's above- and belowground competitive impacts (Christy 1986, Putz and Canham 1992, Horsley 1993, Beckage et al. 2000, Nilsen et al. 2001, de la Cretaz and Kelty 2002). By preempting much of the light and soil resources that would have otherwise been available to seedlings this layer is thought to operate similarly to an overstory canopy (Veblen 1982, Messier et al. 1989, Tappeiner et al. 1991, Dillenburgh et al. 1993, Inderjit and Mallik 1996, Schnitzer et al. 2000, Perez-Salicrup and Barker 2000). Alternatively, a dense understory canopy can lower seedling establishment rates in a manner largely independent of resource

reduction. Specifically, by acting as a favorable microhabitat for seed and seedling predators, this vegetation layer may indirectly decrease seedling recruitment and survival (Burger and Louda 1994, Gill and Marks 1991, Reader 1993, Bonser and Reader 1998). In fact, microhabitat influenced seed and seedling predation mediating what are ostensibly competitive outcomes may be a pervasive, yet generally disregarded indirect effect (Reader 1992, Burger and Louda 1994). This indirect control over seedling recruitment is readily conceptualized through models of apparent competition (Holt 1977, 1984, Connell 1990). In its most fundamental articulation, this model posits that an herbivore's consumption on one plant species increases as a consequence of increased abundance in a second plant species (Holt 1977, 1984). Connell (1990) expanded on this core idea by modeling situations where one plant species need not be consumed by the herbivore, but rather provide a preferred microhabitat for the herbivore. By preferentially utilizing the microhabitat in and around this non-prey species, herbivores increase their consumption on individuals of a second, vulnerable plant species (Figure 3.1a). In both cases, direct competitive interactions from the non-target plant 'appear' to drive the reductions in vulnerable plant abundance when, in fact, the reductions are mediated by herbivory. Application of this theoretical framework to forests containing dense understory layers is straightforward. The presence of a dense understory canopy i) provides a preferred microhabitat for small mammals, ii) increased patch use leads to increased seed and seedling predation, iii) this increased risk alters seedling recruitment patterns among species.

In plant communities, there is ample evidence supporting the three assumptions of the apparent competitive model. First, research has repeatedly confirmed heightened small mammal activity and foraging underneath a dense understory layer (Longland and Price 1991, Kotler et al. 1991, Lidicker et al. 1992, Manson and Stiles 1998). These animals are able to assess risk from

aerial predators and shift their patch usage towards microhabitats that confer protection (Kotler et al. 1991, Kotler et al. 2004, Dall et al. 2001). Second, small mammals are voracious seed and seedling predators often exhibiting distinct food preferences often preferring to consume larger or less defended seeds. (Smith 1972, Kantak 1983, Wolff et al. 1985, Bucyanayandi et al. 1990, Ostfeld and Canham 1993, Hulme 1994, Ostfeld et al. 1997, Ivan and Swihart 2000). Finally, pervasive and preferential predation can lead to rapid changes in plant community composition and impede tree regeneration (Ostfeld and Canham 1993, 1997, Reader 1997, Schnurr et al. 2004).

In spite of the repeated evidence documenting the importance of small mammal seed and seedling predation in natural systems ranging from grasslands to deserts, boreal forests, and old-fields (Brown and Heske 1990, Gill and Marks 1991, Wada 1993, Hulme 1994, Ostfeld and Canham 1993, Reader 1993, Ostfeld et al. 1997, Bonsor and Reader 1998, den Ouden 2000, Manson et al. 2001, Kotler et al. 2004, Schnurr et al. 2004), we know only two tests that experimentally assess the importance of resource competition relative to predation in forest communities (Cornett et al. 1998, Beckage and Clark 2005). One test (Cornett et al. 1998) does not factorially manipulate the presence and absence of both understory cover and predator access thus precluding the decoupling of competition from apparent competition. Given the increased occurrence of dense understory vegetation layers in forests worldwide (Royo and Carson, *in review*) and the ubiquity of small mammal predation (reviewed by Hulme 1998), understanding their interaction is critical as tree seedling establishment beneath an understory canopy may not hinge simply on shade tolerance, but instead be modified by predation risk.

We investigated the direct competitive effect of hay-scented fern (*Dennstaedtia punctulobula* (Michx.) Moore) cover and the direct consumptive effect by small mammals on

trees seedling establishment. Furthermore, we tested the interaction between presence of cover and small mammal predation, specifically the indirect apparent competitive effect. We experimentally altered canopy cover and small mammal access to test 1) whether small mammal activity is greatest underneath fern cover, 2) if hay-scented fern exerts a direct competitive effect on seedling establishment, and 3) to what extent is there an apparent competitive effect of hay-scented fern cover on tree seedling establishment via mediating higher seed or seedling predation. We further explored small mammal preferences for seeds of various hardwood tree species and how predation rates differed between microhabitats.

### **3.3 METHODS**

#### **3.3.1 Research Sites**

We conducted our study at three Allegheny hardwood sites within the Allegheny High Plateau Region of northwestern Pennsylvania. The vegetation structure is characterized by a black cherry and red maple (*Acer rubrum* L.) dominated canopy, little tree regeneration in the sapling and pole size classes, and an understory dominated by hay-scented fern. Forests in the Allegheny region experience a cool and humid climate with an average summer temperature of 18.9 °C and an annual precipitation of 109 cm (Lutz 1930, Whitney 1990). Two sites, Marienville (MV) and Long Run (LR), are managed by Kane Hardwood Company. The third site, Clermont (CL), is managed by Forest Investment Associates.

#### **3.3.2 Understory Layer**

Hay-scented fern is a rhizomatous perennial with 30- to 74 cm tall fronds (Cody et al. 1977). This species is impalatable to deer and exhibits aggressive vegetative growth with increased understory light levels (Cody 1977, Royo *unpub. data*). Consequently, increased logging coupled with deer overbrowsing of alternative, palatable vegetation has dramatically increased

hay-scented fern cover over the past several decades (de la Cretaz and Kelty 1999, Horsley et al 2003). In the Allegheny region, this species historically represented approx. 1.0 – 3.3 % of the understory cover (Lutz 1930) and presently covers an estimated 33% of the forest understory (Royo, unpub. data). Once established, hay-scented fern severely inhibits tree establishment, growth, and survival (Horsley and Marquis 1983, Drew 1988, Horsley 1993, George and Bazazz 1999 a,b). This extensive and nearly monodominant understory layer is typical of many forest understories worldwide (e.g. rhododendron thickets in SE U.S., Monk et al. 1985; ericaceous heaths in boreal forests, Mallik 2003).

### **3.3.3 Experimental Design**

At each of the three sites we established five blocks each containing the four, 4 m<sup>2</sup> treatment plots with 2 x 2 factorial manipulations of fern cover using herbicide and small mammal predation using exclosures. We eliminated fern cover using an herbicide application (Accord<sup>tm</sup> and X-77<sup>tm</sup> surfactant) at the recommended rate for this forest cover type of 1.15 kg of active ingredient per hectare (Horsley 1981) to create 4 m<sup>2</sup> gaps in the fern canopy. We manipulated predator access by constructing 1 meter tall exclosures using 1cm<sup>2</sup> hardware cloth inserted into the ground ~25 cm with 25 cm tall plastic flashing around each base. Hardware cloth lids prevented squirrels and chipmunks from entry. The resulting treatments were i) Control, ii) No Fern Cover, iii) No Small Mammals, iv) Neither Fern Cover nor Small Mammals (Figure 3.2). This design replicated at three sites across the plateau allows us to rigorously decouple the direct effects of competition and predation and test for any apparent competitive interaction.

### **3.3.4 Sampling Regime**

We used Sherman live traps (Sherman Traps, Tallahassee, FL, USA) baited with a peanut-butter and oatmeal mix to assess small mammal activity in the fall of 2002 and continuing in summers



2003 and 2004. At each trapping date we placed one trap on the inside perimeter of each plot (20 traps/site) for a 24 hr period. Captured animals were identified and released. We trapped on five dates in fall 2002 following to assess exclosure efficacy and remove any remaining animals from within the exclosures. We further trapped from late May until Late August in both 2003 and 2004 on 12 dates at 2 – 3 week intervals. In total, each site was trapped 13 – 15 times, for a total of 810 trap-nights. The mean capture rate (# captures/100 trap-nights) per treatment was used as a measure of small mammal activity (Wilson et al. 1996).

Individual seedling germination and survival were monitored in the center 1m<sup>2</sup> of each 4m<sup>2</sup> plot in June 2003 and 2004 using colored plastic binder rings to identify each cohort. Thus, we have recruitment, by species, for 2003 and 2004, as well as one-year survival for the 2003 cohort. As initial conditions were heavily dominated by black cherry, we transplanted five sugar maple seedlings (*Acer saccharum* Marsh.) and five red maple seedlings into each treatment plot to expand our ability to infer treatment effects on other species. Red maple seedlings were grown in a greenhouse using standard, unfertilized potting mix and artificially stratified seed from local seed stock (Sheffield Seed Supply, Locke, NY). Seed was stratified for 67 days in moist peat moss. Sugar maple seedlings were collected from naturally germinating individuals in a sugar maple stand located central to all three field sites. Collected seedlings did not receive any fertilizer and were transplanted directly into the field in late May 2003. Red maple seedlings had a mean height of 4.0 cm and sugar maple seedlings had a mean height of 7.0 cm. The initial survival (approx. three weeks) of all transplanted seedlings was assessed during the overall seedling census of June 2003 to evaluate transplant shock.

Finally, we conducted small mammal feeding trials at four dates from late July to early September 2003 to determine if seed predation varied among different microhabitats and among

species. Seeds of five species: red maple, white ash (*Fraxinus americana* L.), sugar maple, black cherry, and beech (*Fagus grandifolia* Ehrh.) were included to represent species found in this forest type. These five species span both the range of shade tolerance (beech > sugar maple > red maple > black cherry > white ash; Burns and Honkala 1990) and seed size (beech > black cherry > sugar maple > white ash > red maple; U.S. Forest Service 1989). In each plot, we placed five seeds of each species in aluminum screen dishes (25 seeds/tray) and monitored seed removal rates over a 24 hour period (0, 4, 16, and 24 hours after introduction). We ended each trial after 24 hours as the majority of seeds were removed within this time period. We discontinued sampling at five plots which were completely destroyed following a major windstorm in the region on July 23rd 2003.

### **3.3.5 Statistical analysis**

We tested the effect of Site Block, Fern Cover, and Exclosure as well as their interactions on the response variables (small mammal capture rate, emergence, survival) using ANOVA. Furthermore, we conducted orthogonal contrasts to isolate and test the effect of competition, predation, and apparent competition without any confounding between them. Specifically, we tested: i) Competition (fern cover vs. no fern cover in the absence of any predation), ii) Predation (small mammal predators vs. no small mammal predators in the absence of fern cover), and iii) Apparent Competition (fern cover exposed to predation vs. fern cover devoid of predation) (Figure 3.2). Prior to analyses, emergence data were square-root transformed and survival data were arcsine transformed to satisfy the assumptions of ANOVA (Sokal and Rohlf 1995). Finally, tests to differentiate among the five seed species in the preference trials utilized Bonferroni pair-wise comparisons. We conducted all statistical analyses using SAS <sup>TM</sup> statistical software (SAS Institute 2004).

## 3.4 RESULTS

### 3.4.1 Small mammal activity

The exclosures significantly reduced the presence of small mammals ( $F = 98.88$ ,  $P < 0.0001$ ) primarily deer mice and white-footed mice. We caught a total of 16 small mammals within the exclosures vs. 93 in the controls. Furthermore, small mammal mean capture rate in unfenced plots with fern cover ( $\bar{x} = 32.16$  captures/100 trap-nights) was significantly greater ( $F = 42.3$ ,  $P < 0.0001$ ) than unfenced, fern-free plots ( $\bar{x} = 13.65$  captures/100 trap-nights). Although small mammal abundances vary across years in response to food availability (e.g. Schurr et al. 2002), our capture rates fall within the range of other trapping data in the region (range 1 – 30;  $\bar{x} = 13$  captures/100 trap-nights; Stoleson *unpub. data*).

### 3.4.2 Tree seedling recruitment and establishment

Establishment patterns varied between the two dominant canopy tree species, black cherry and red maple. After two years, black cherry mean seedling densities were greatest in plots with neither fern cover small mammal access ( $\bar{x} = 18.52$  seedlings/m<sup>2</sup>) and lowest in the control plots ( $\bar{x} = 4.57$  seedlings/m<sup>2</sup>). Black cherry emergence was greater within exclosures (Table 3.1a; Figure 3.3) and small mammal seed predation significantly reduced black cherry emergence in both 2003 and 2004 (Table 3.1b; Figure 3.3a). Fern cover did not reduce the emergence of black cherry in either year (Table 3.1a; Figure 3.3a). Hay-scented fern cover did, however, exert an apparent competitive effect on black cherry with significantly greater seedling densities in fern covered plots devoid of predators relative to fern cover plots exposed to predators (Table 3.1b; Figure 3.3a). Finally, black cherry survival from 2003 – 2004 was unaffected by predation, direct competition, or apparent competition (Tables 3.1 a,b; Figure 3.4a).

Red maple density averaged fewer than five seedlings/m<sup>2</sup> in 2003, but increased nearly 600% from 2003 following a mast event (Figure 3.3b). This mast event was particularly acute at one site (Clermont) with emergence increasing ten-fold from 2003. Red maple seedling densities by 2004 were greatest in unfenced plots without fern ( $\bar{x} = 45.42$  seedlings/m<sup>2</sup>) and lowest in fenced plots with fern ( $\bar{x} = 15.07$  seedlings/m<sup>2</sup>). Red maple emergence was reduced by direct competition from hay-scented fern cover with the difference being significant in 2003 and marginally significant in 2004 (Table 3.1b; Figures 3b). Red maple seedling survival was significantly lowered by direct competition from hay-scented fern cover (Table 3.1b; Figure 3.4b). Finally, neither seed predation nor apparent competition reduced red maple emergence or seedling survival (Table 3.1b).

Transplanted sugar maple seedlings experienced some initial mortality within the first three weeks of being transplanted with unfenced areas suffering greater mortality than fenced areas. Often, herbivores clipped, but did not consume, seedlings. This pattern of decreased survival in fern covered plots open to predation ( $\bar{x} = 0.56 \pm 0.08$ ) relative to fern covered plots within exclosures ( $\bar{x} = 0.89 \pm 0.05$ ) indicate an apparent competitive effect on their initial survival ( $F = 20.7$ ;  $P < 0.001$ ). Following this period of initial mortality, sugar maple seedlings experienced relatively high survival (aprox. 70%) in their first year regardless of treatment (Table 3.1; Figure 3.4c).

### **3.4.3 Seed predation on different species and in different microhabitat**

Rates of overall seed removal within the fences was negligible (< 2%). As a result, we focused our analyses on the contrast among species between the unfenced, fern-covered plots and the unfenced, fern-free plots. Seed removal rates significantly differed among sites, among species, and between microhabitats (Table 3.2). Seed removal rates differed significantly among sites

with the greatest percentage of seeds removed in Marienville and Clermont ( $88\% \pm 2.02$  for both sites) and lowest at Long Run ( $77\% \pm 3.05$  for Marienville, Clermont, and Long Run, respectively). Beneath fern cover, seed removal was significantly greater ( $96\% \pm .009$ ) than fern-free areas ( $73\% \pm .024$ ). Post-hoc Bonferroni analyses to detect preferences among seed species yielded a preference hierarchy of beech > black cherry > maples > white ash (Figure 3.5); however, this hierarchy was significantly different only in the fern-free plots (Table 3.2; Figure 5b).

### **3.5 DISCUSSION**

#### **3.5.1 Disentangling competition from apparent competitive**

We found hay-scented fern cover exerts both direct competitive and indirect, apparent competitive effects on tree seedling establishment. Apparent competition was responsible for significantly reducing black cherry emergence in control plots relative to fern covered plots protected from predators. Emergence was not only consistently lower beneath fern in both 2003 and, but it was also consistent across sites (e.g. lack of significant site\*fence effect). Our experimental design allowed us to rigorously parse out the effects of competition, predation, and apparent competition without confounding among them (Reader 1992). Prior work documenting decreased cherry seedling densities in fern-covered areas relative to fern-free areas (e.g., Lyon and Sharpe 1995, George and Bazzaz 1999 a,b, de la Cretaz and Kelty 2002) has attributed the difference primarily to above-ground competition by fern (Horsley et al. 1993). This study provides the first evidence that indirect apparent competitive interactions, rather than direct competitive interactions, initiate this pattern of decreases seedling densities under fern by reducing emergence.

By contrast, neither predation nor apparent competition had any effect on red maple. Although mammals readily consume seeds and seedlings of red maple (Figure 3.5; McCracken et al. 1999, Schnurr et al. 2002), we attribute the lack of a predation effect to at least two reasons. First our seed removal trials suggest that red maple is less preferred than black cherry, and thus, potentially less limited by predation. Second, differences in timing of seed set relative to the perennial hay-scented fern cover may explain the lack of an effect. Hay-scented fern fronds begin to emerge in early May with peak height and density occurring from July into September (Horsley 1993, Hill and Silander 2001). Peak black cherry dispersal is from August to September (Marquis 1990), a period when the fern canopy is still present to provide suitable microhabitat for small mammals. Conversely, red maple disperses in spring and early summer (Walters and Yawney 1990). Consequently, many of these seeds disperse onto a forest floor without fern cover is not yet fully expanded and; therefore, cannot provide the microhabitat to mediate higher mammal activity and predation.

These differences in phenology may also account for the strong competitive effect of hay-scented fern on red maple emergence, but not black cherry. Black cherry exhibits an early germination strategy beginning in early to mid April (Marquis 1973, Horsley 1993), thereby escaping the increasingly dark conditions caused by hay-scented fern emergence and expansion (Hill 1996). Conversely, red maple's spring dispersal results in a protracted germination period extending into summer (Walters and Yawney 1995). Thus, the prolonged germination strategy of red maple exposes a subset of its germinating seeds to suppression by a dense fern cover (George and Bazzaz 1999a).

Sugar maple experienced relatively high mortality in the first three weeks following planting; however we do not believe transplant shock is the cause as individuals within the

exclosures had a nearly 90% survival during this brief period. Rather, in unfenced areas, we observed that 14 – 17% of the seedlings were clipped at the base by animals but not consumed. We do not interpret this result as a consumptive impact of small mammals over seedling composition as all the mammals trapped are mainly granivorous. We suggest that animal curiosity may generate this phenomenon. Others have previously noticed this ‘curiosity’ driven, non-consumptive mortality in old fields and forests (e.g., Gill and Marks 1991, Horsley 1993). Nonetheless, this initial mortality pattern also supports the apparent competition hypothesis as mortality via clipping was significantly greater in control plots relative to fern covered plots within exclosures. The remaining sugar maple individuals exhibited the relatively high survival, even under the dense fern canopy, characteristic of a very shade tolerant species (Figure 3.4c; Godman et al. 1990).

### **3.5.2 Comparison to other studies**

Several studies of post-dispersal seed predation in areas with dense understory cover hint at a potential for apparent competition; however, the experimental designs typically confound competitive impacts with predation (Reader 1992). Some studies utilize correlative methods (e.g., Manson et al. 2001) or comparisons of seed removal rates between areas with cover and those without (Wada 1993, Den Ouden 2000, Iada 2004) to assess the influence of microhabitat on seed and seedling predation. Others report on manipulations of understory cover or small mammal predation, but few studies do both simultaneously. Studies that manipulate predation reveal substantial seed and seedling predation and further suggest this loss is exacerbated beneath herb or shrubby cover (Manson and Stiles 1998, Edwards and Crawley 1999, Clark and Wilson 2003, Sun et al. 2004). Alternatively, studies that manipulate microhabitat find predation

rates decline following removal of vegetation cover (Manson and Stiles 1998, Schreiner et al. 2000, Kollman and Buschor 2002).

Only a handful of studies manipulate cover and predation simultaneously to disentangle competitive effects from predation effects. Among the first was work by Gill and Marks (1991) who erected an exclosure around the perimeter of their entire experiment and thus argued that any reductions in tree seedling establishment observed under herbaceous cover were due solely to competition. They further concluded that the intensity of microhabitat-mediated small mammal predation was “unexpected” calling it a “novel mechanism” of tree recruitment inhibition by understory plants. More recently, Reader (1993) and Bonser and Reader (1998) utilized a 2 x 2 factorial design to examine the independent and interactive effects of competition and predation. Although their work was focused on the short-term (<1 yr) emergence of old field species preyed upon by invertebrates, their results are entirely consistent with our findings. Larger-seeded species experienced greater emergence within the exclosures and (Reader 1993) and specifically, vegetation cover ‘indirectly’ lowered the emergence of larger seeded species by facilitating higher predation (Bonsor and Reader 1998). In forest systems, Cornett et al. (1998) used an incomplete factorial study with control, fenced-unweeded plots, and unfenced-weeded plots. Although the authors argue this design tests for competition and seed predation, clearly these comparisons are confounded (e.g. fenced plots exclude predators but still contain vegetation cover). Nevertheless, the data demonstrate emergence and survival for both balsam fir and white pine is increased within the fenced-unweeded plots relative to control plots suggesting strong apparent competitive effects. Finally, Beckage and Clark (2005) assessed the importance of rhododendron cover and small mammal predation on seedling emergence in Appalachian forests using a complete 2 x 2 factorial design. They found northern red oak and



red maple emergence under rhododendron cover was significantly enhanced within exclosures, supporting the apparent competition model. All of the above examples are bolster our assertion that dense vegetation layers can suppress seedling establishment via indirect, apparent competitive interactions. Indeed, we suggest all these cases could be conceptualized under a simple, yet realistic, extension of Connell's (1990) apparent competition model (Figure 3.1b). This variant would specifically model the apparent competitive effect of a dense herbaceous or shrubby layer on multiple woody tree prey species by mediating higher predation.

Our seed removal trials confirmed that small mammals exhibit distinct seed preference with beech and black cherry being the most preferred and ash least preferred. The strength of these preferences are likely by various factors including chemical composition, seed coat thickness, seed density (availability), and seed mass (Rey et al. 1997, Kollmann et al. 1998, Hulme and Borelli 1999). Our preference rankings (beech > black cherry > maples > ash) are generally consistent with the seed mass rankings (beech > black cherry > sugar maple > ash > red maple; U.S. Forest Service 1989). Others have demonstrated a seed predator preference towards larger seeded species (Hulme 1994, Wolff et al. 1995, Reader 1997, Ivan and Swihart 2000; but see Moles et al. 2003) as well as a preference towards *Prunus* spp. (Kollmann et al. 1998) and an aversion to ash (Hulme and Hunt 1999, Hulme and Borelli 1999). The rejection of the intermediately sized white ash over red maple may be due, in part, to the high phenolic content in ash seeds (Jensen 1985, Hulme and Hunt 1999, Hulme and Borelli 1999). Alternatively, red maple preference may result from the experimental design, and not truly reflect preference. We conducted our seed removal trials in the late summer and fall although this species sets seed in the spring. Therefore, presenting this species to predators in the fall may represent a novel food item (Meiners and LoGiudice 2003).

### **3.5.3 Role of post-dispersal seed predation in forest regeneration**

There are several critiques regarding the importance of rodent post-dispersal seed predation decreasing tree recruitment. First, removal does not necessarily equate with predation as some portion of the seeds is not immediately consumed but rather, dispersed, cached, and subsequently germinates (e.g. Theimer 2001). Nevertheless, researchers have found that small mammals i) locate and consume the vast majority of seeds deposited in caches, and ii) often cache seeds in microsites unsuitable for germination or seedling survival (reviewed by Vander Wall 1993 and Hulme 1998). Other researchers stress the importance of masting events as a mechanism to satiate the available granivore population and allow seedling recruitment (Silvertown 1980, Sork 1993, Vander Wall 2002). In fact, the degree to which small mammals determine seedling recruitment patterns can vary spatially and temporally depending on the relationship between seed production (resource) and small mammal population (e.g. Ostfeld et al. 1994, McCracken et al. 1999, Schnurr et al. 2002). Nonetheless, we argue that the importance of these recruitment opportunities may be overstated, particularly in forests containing a dense understory layer. First, the escape of a portion of seeds by caching or satiation does not mean small mammals have “no effect” on seedling emergence as overall recruitment could be even greater in the absence of predators (Hulme 1998). Additionally, in areas covered by a dense herb or shrub stratum, not only is predation intensified, but the small numbers of seeds that do manage to germinate emerge into a highly shaded environment inimical to survival and growth.

### **3.5.4 Conclusion**

Our results indicate that a dense understory vegetation layer can exert both direct competitive and indirect, apparent competitive effects on seedling emergence and survival in forests and that these effects vary across species and life-history stages. This work reveals that indirect

mechanisms can play an important role in lowering emergence rates and altering recruitment patterns that are ostensibly structured by direct competitive interactions. We predict that in forests containing a dense understory layer, most tree species will experience an ongoing cycle of germination and mortality that reduces successful recruitment into the advance regeneration layer. The dual constraints of competition and apparent competition will greatly the diversity and abundance of seedlings available to capitalize on the unpredictable, gap-driven growth opportunities. The importance of these co-occurring mechanisms may be common, particularly as the development of dense understory vegetation layers is becoming increasingly common across forests worldwide (Royo and Carson, *in review*).

**Table 3.1 ANOVA Table on Germination and Survival.**

A. Analysis of Variance results from the 2 x 2 factorial manipulations of fern cover and small mammal exclosures on black cherry, and red maple germination and survival, and transplanted sugar maple survival. B. Orthogonal contrasts testing i) predation (exclosures +/- without any fern cover), ii) competition (fern cover +/- within exclosures), ii) apparent competition (fern cover within exclosure vs. control). P values significant at the < 0.05 level are printed in bold.

**A**

Factors	Black Cherry Germination 2003		Black Cherry Germination 2004		Black Cherry Survival		Red Maple Germination 2003		Red Maple Germination 2004		Red Maple Survival		Sugar Maple Survival	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Site	0.03	0.973	0.99	0.429	0.04	0.966	0.9	0.547	2.1	0.237	3.41	0.277	0.69	0.629
Block(Site)	<b>16.44</b>	<b>&lt;0.0001</b>	<b>3.61</b>	<b>0.002</b>	1.86	0.087	<b>2.14</b>	<b>0.037</b>	<b>5.1</b>	<b>&lt;0.0001</b>	1.73	0.112	0.5	0.888
Fern	0.75	0.477	6.56	0.123	12.47	0.071	9.88	0.088	4.93	0.156	<b>476.76</b>	<b>0.001</b>	0.01	0.919
Exclosure	14.21	0.064	<b>21.74</b>	<b>0.042</b>	0.22	0.687	0.13	0.753	0.23	0.677	0.89	0.445	0.03	0.879
Fern*Exclosure	0.89	0.351	0.02	0.884	1.14	0.294	2.34	0.135	1.16	0.289	0.06	0.8	0	0.978
Site*Fern	3.22	0.052	0.81	0.455	0.63	0.537	0.23	0.797	<b>4.46</b>	<b>0.019</b>	0.11	0.897	1.68	0.204
Site*Exclosure	1.55	0.973	1.05	0.36	0.5	0.612	0.76	0.474	<b>15.07</b>	<b>&lt;0.0001</b>	2.31	0.116	1.72	0.198
Site*Fern*Exclosure	<b>5.06</b>	<b>0.011</b>	1.85	0.173	0.64	0.534	0.01	0.987	0.83	0.446	0.25	0.777	0.75	0.481

**B**

Hypotheses	Black Cherry Germination 2003		Black Cherry Germination 2004		Black Cherry Survival		Red Maple Germination 2003		Red Maple Germination 2004		Red Maple Survival		Sugar Maple Survival	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Predation vs No Predation	<b>5.3</b>	<b>0.026</b>	<b>9.4</b>	<b>0.004</b>	0.34	0.585	0.81	0.372	2.35	0.134	1.079	0.305	0.05	0.829
Competition vs No Competition	0.14	0.71	2.28	0.139	1.5	0.228	<b>5.08</b>	<b>0.029</b>	3.97	0.054	<b>27.42</b>	<b>&lt;0.0001</b>	0.05	0.669
Apparent Competition	<b>11.99</b>	<b>0.001</b>	<b>12.02</b>	<b>0.001</b>	1.12	0.296	1.88	0.178	0.21	0.649	0.825	0.37	0	0.9543

**Table 3.2 ANOVA table on seed preference trials.**

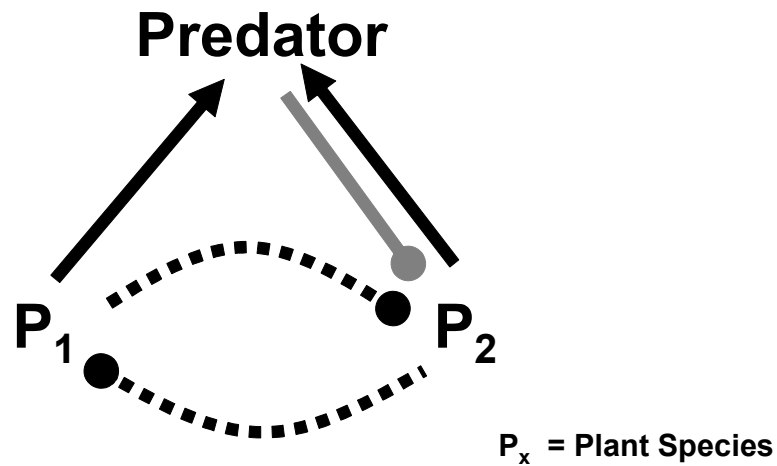
Analysis of variance results of fern cover on seed removal among different species, p values significant at the  $< 0.05$  level are printed in bold.

<b>Factors</b>	<b>Seed Removal</b>	
	<b>F</b>	<b>P</b>
Site	<b>3.99</b>	<b>0.047</b>
Block(Site)	<b>3.68</b>	<b>&lt;0.0001</b>
Fern	<b>113.38</b>	<b>&lt;0.0001</b>
Species	<b>21.08</b>	<b>&lt;0.0001</b>
Fern*Site	<b>5.52</b>	<b>0.0042</b>
Species*Fern	<b>5.22</b>	<b>0.0004</b>
Species*Site	0.66	0.727
Species*Fern*Site	1.17	0.315

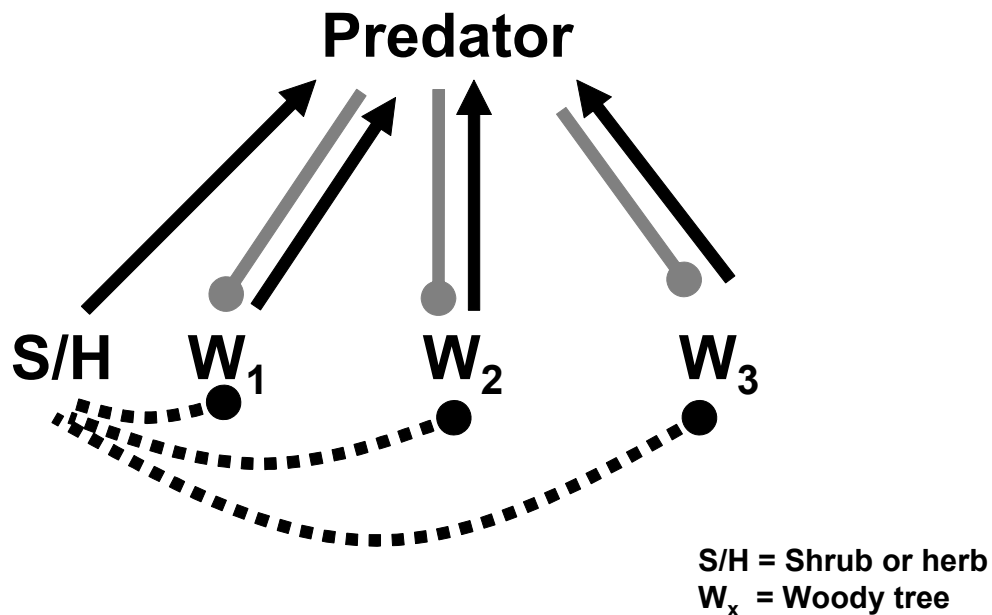
### Figure 3.1 Models of microhabitat-mediated apparent competition

Solid lines are direct interactions, dashed lines indicate indirect interactions. Arrowheads indicate a positive effect on species, circle indicates negative effects. A). Adaptation of Connell's (1990) model in which  $P_1$  provides a favorable habitat for the predator who only consumes individuals of  $P_2$ , adapted from Connell (1990). B). Simple, but realistic extension of model for forest understories containing a dense herbaceous (H) or shrubby (S) layer in which the understory layer (S/H), provides a favorable habitat for predator who consumes a variety of woody ( $W_x$ ) species.

a

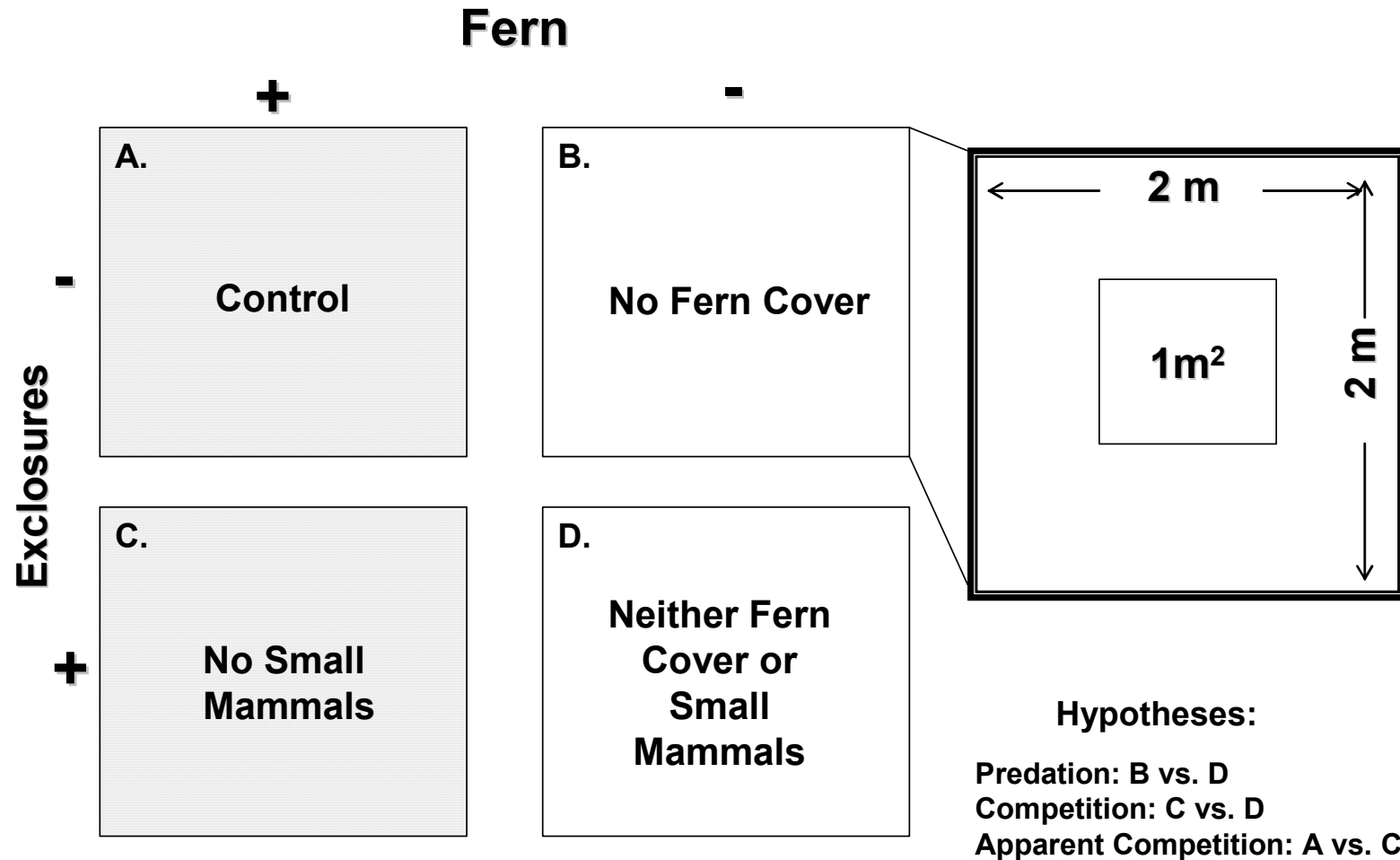


b



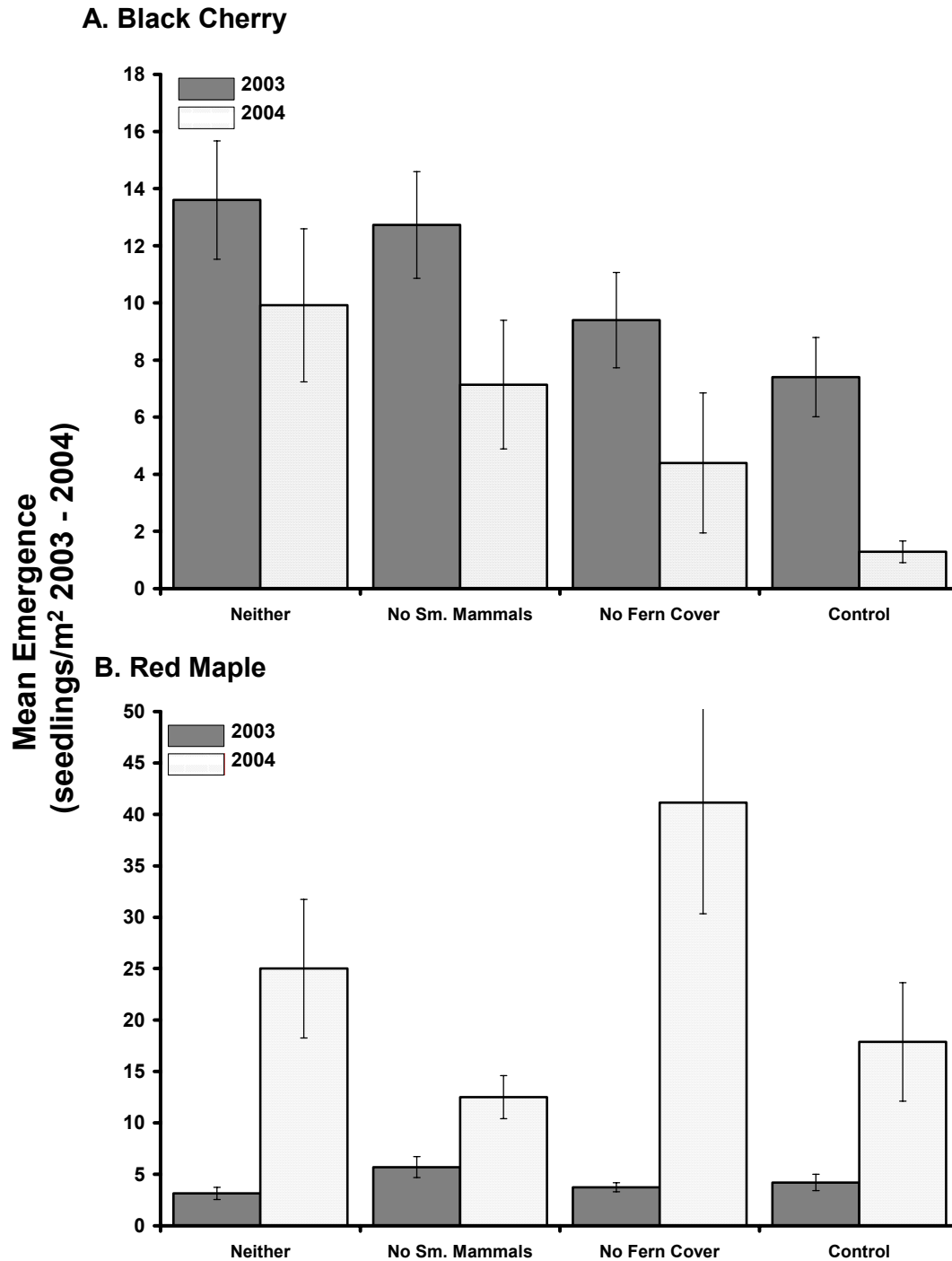
**Figure 3.2 Schematic of experimental design.**

A 2 X 2 factorial with fern cover and small mammal manipulations (presence or absence). Shading represents fern cover left intact. Specific hypotheses tested using orthogonal contrasts are: predation (no fern cover vs. neither), competition (no small mammals vs. neither), and apparent competition (control vs. no small mammals).



**Figure 3.3 Effect of small mammal predation and fern cover on germination.**

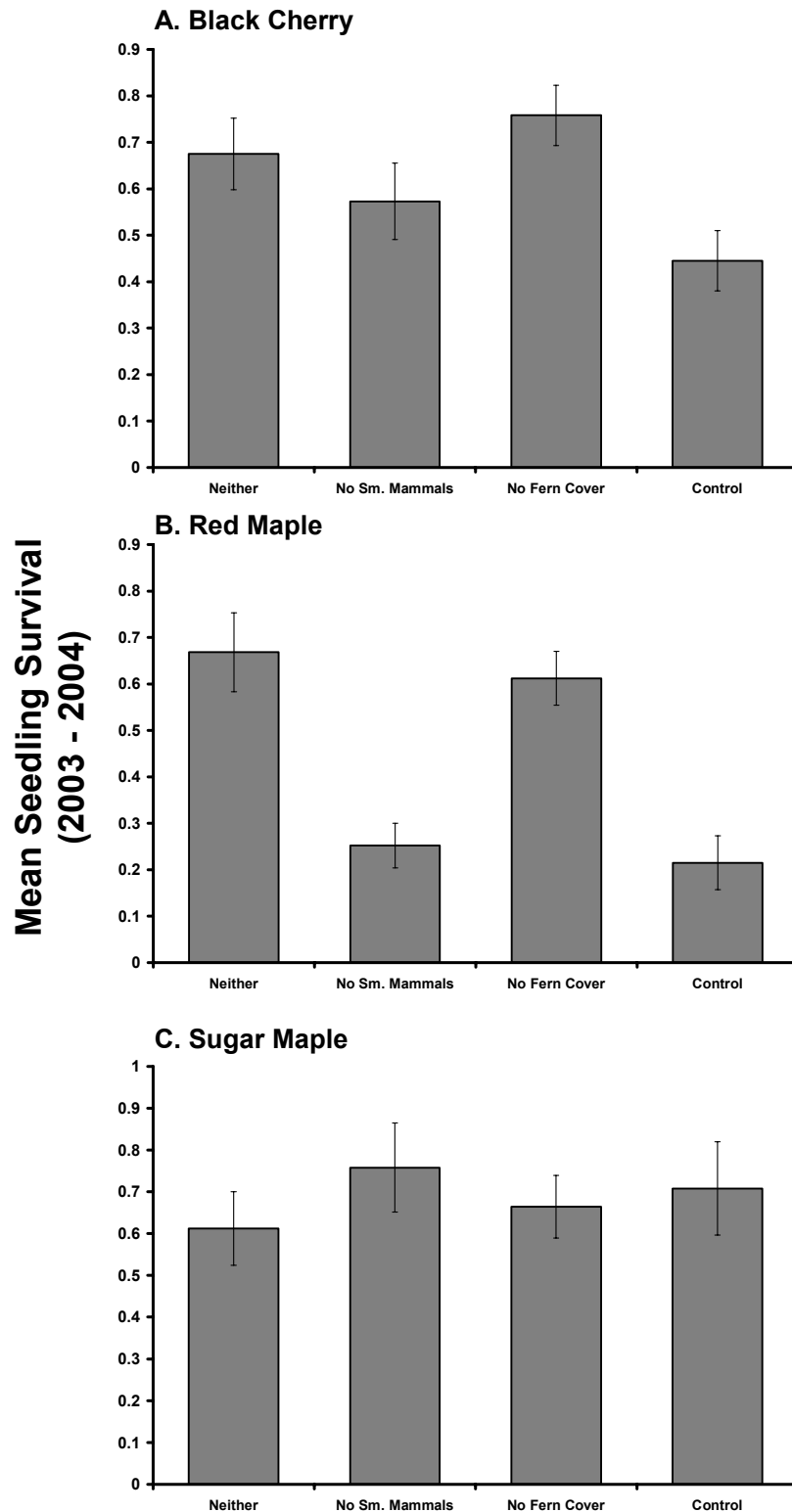
Small mammal predation and fern cover effects on germination of A) Black Cherry and B) Red Maple seedlings in 2003 and 2004. Bars represent means  $\pm$  1SE. Refer to Table 1 for ANOVA results.





**Figure 3.4 Effect of small mammal predation and fern cover seedling survival.**

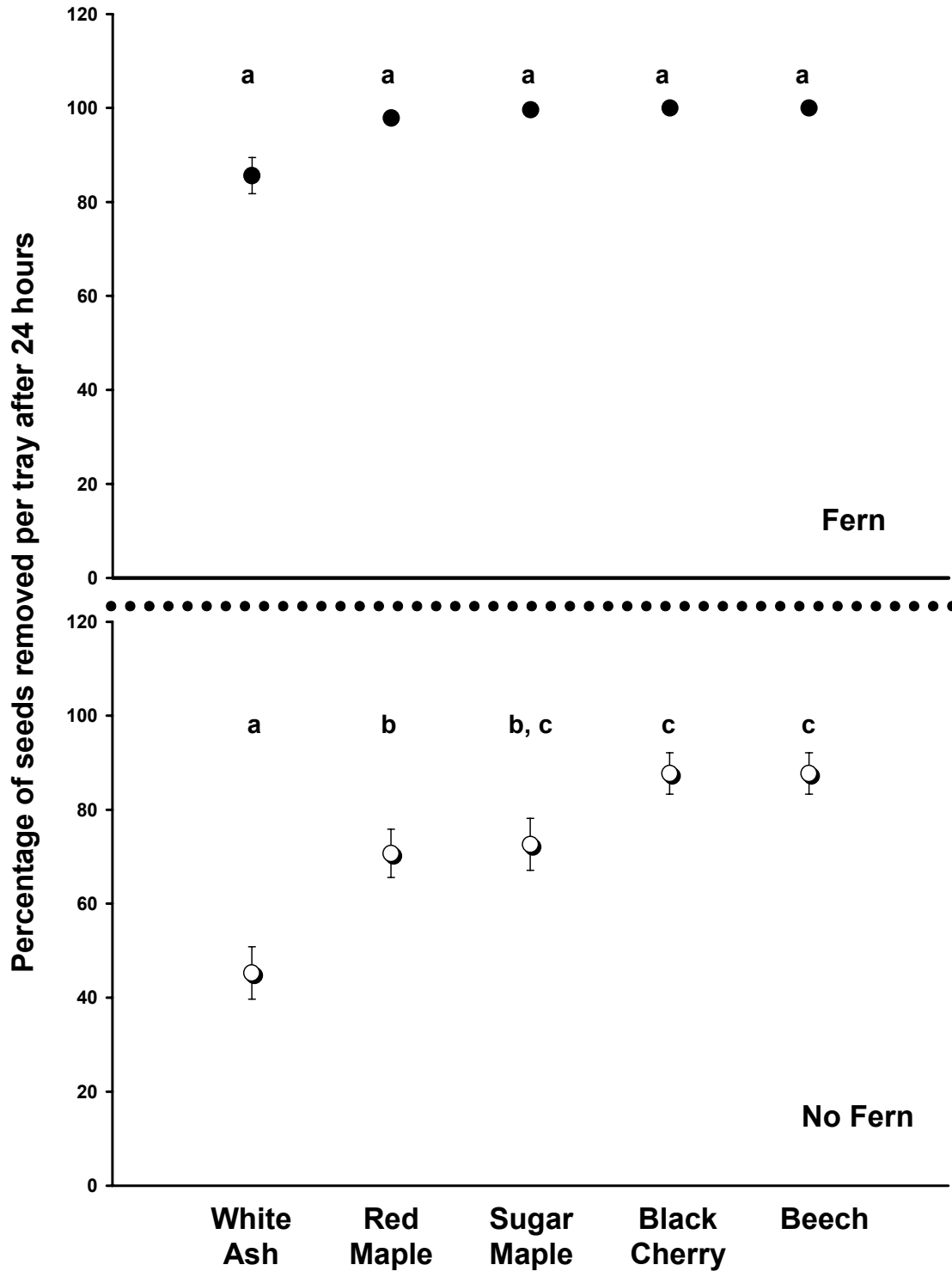
Effect of small mammal predation and fern cover on the first year survival of the 2003 seedling cohorts of A) Black Cherry, B) Red Maple, and C) Sugar Maple. Bars represent means  $\pm$  1SE. Refer to Table 1 for ANOVA results.



**Figure 3.5 Mean proportion of seeds removed by species.**

Mean proportion of seeds removed by species in fern covered plots (- ● -) and fern-free plots

(- ○ -). Bars represent means  $\pm 1$ SE. Letters denote significant differences among species (Bonferonni adjustment;  $P < 0.05$ ).



## **4.0 MARCH TOWARDS MONODOMINANCE: DEER, FERN, AND THE FUTURE OF ALLEGHENY HARDWOOD FORESTS**

### **4.1 ABSTRACT**

In forests, empirical work has repeatedly demonstrated that herbivory and competition from dense understory plant layers can alter tree seedling composition, distribution, and abundance patterns. Furthermore, as plants in the understory frequently experience herbivory and competition simultaneously, there exists the possibility for these two factors to interact. Despite this, research assessing the effect of competition and herbivory rarely examines potential interactions between the two factors. Additionally, forest management decisions that mitigate the impact of one factor without regard for the other often fail in achieving diverse regeneration. We experimentally investigated the independent and synergistic effects of white-tailed deer (*Odocoileus virginianus*) herbivory and understory plant competition in forests harboring an overabundant deer herd and containing an understory extensively covered by hay-scented fern (*Dennstaedtia punctilobula*). We hypothesized that deer browsing would decrease overall seedling densities and shift seedling composition towards species that are browse tolerant or unpalatable. We further hypothesized that the dark conditions found under a dense fern canopy would decrease seedling densities and limit species composition to only the most shade tolerant species. Conversely, excluding deer and creating gaps in the fern canopy would increase overall seedling densities and allow a recruitment opportunity for browse-intolerant and shade-intolerant tree species, respectively. To test these hypotheses we paired six, 14 X 20 meter exclosures with

control plots at each of three sites across northwestern Pennsylvania and created gaps in the fern canopy of six different sizes (control, 1 m<sup>2</sup>, 2.5 m<sup>2</sup>, 3.75 m<sup>2</sup>, 5 m<sup>2</sup> and 6.25 m<sup>2</sup>) within each plot. We monitored recruitment and survival of all woody species in 1 m<sup>2</sup> subplots centered within each fern gap from 2001 – 2004. Over the course of four years we found that fern gaps significantly increase the recruitment of pin cherry and birch as well as the survival of black cherry, red maple, and pin cherry. This increase in emergence and survival significantly increased species richness and density in fern gaps but did not enhance diversity or reduce the proportion of plots dominated by black cherry seedlings. Seedling height did not significantly increase with the majority of seedling remaining under 15 cm tall suggesting that light underneath an intact overstory canopy remained limiting for growth. We found deer herbivory had neither independent nor synergistic effects with fern cover on seedlings of this size. Nonetheless, we suggest that nearly a century of deer overabundance has yielded a forest community legacy in which unpalatable plant species, namely hay-scented fern and black cherry, prevail. This legacy predisposes much of the contemporary forests in the region to ever increasing monodominance by either fern or black cherry. This study suggests that, left unmanaged, long-term forest dynamics in the Allegheny Plateau will lead to increasingly depauperate forest communities. Consequently, forest management practices that promote the establishment and growth of diverse regeneration may not only be useful, but perhaps indispensable, in order to curb the trend toward increasing monodominance.

## 4.2 INTRODUCTION

There is a growing awareness among ecologists for the need to discriminate among multiple ecological factors and assess their relative importance in structuring natural communities (Harper 1977, Sih et al. 1985, Welden and Slauson 1986, Schoener 1983). In plant communities, empirical work has repeatedly demonstrated that predation (i.e. herbivory and granivory) and competition are typically the preeminent factors determining plant species' establishment and growth (reviewed by Connell 1983, Schoener 1983, Sih et al. 1985, Crawley 1990). Because species often experience the effects of herbivory and competition concurrently, there is potential for these two forces to interact (Gurevitch et al. 2000, Chase et al. 2002). Despite this, most research assesses the effect of competition and herbivory independently and rarely investigates potential interactions between the two factors, particularly in plant communities (Sih et al. 1985, Gurevitch et al. 2000, Chase et al. 2002, Hamback and Beckerman 2003). A review by Sih et al. (1985) found only 6 studies that manipulated both competitors and herbivores in a fully factorial fashion to elucidate their independent and interactive effects on plant species performance. More recently, Hamback and Beckerman (2003) located only 16 plant-herbivore studies that included a fully factorial design on plant population measures and none that scaled up to explore community-level consequences. Clearly, the independent and synergistic roles herbivory and competition play in structuring plant communities remains lacking (Chase et al. 2002).

Research examining tree species distribution and abundance in forest communities typically neglects the role of herbivores and understory competitors and focuses primarily on the gap-phase successional paradigm (Runkle 1981, 1982, Denslow 1987, Uhl et al. 1988, Houle 1990, Oliver and Larson 1996, Marks and Gardescu 1998, Greene et al. 1999, Antos et al. 2000, McCarthy 2001). This theoretical framework predicts that the interplay between overstory gap

size (i.e. light availability) and the shade tolerance of seedlings and saplings is fundamental in determining successional outcomes (Runkle 1989, Canham 1989, Pacala et al. 1996, McCarthy 2001). Implicit within this framework is the assumption that the seedling and sapling layer is diverse and well developed (Kobe et al 1995, Pacala et al. 1996). Nonetheless, herbivory from overabundant deer herds and light competition from understory plants both operate well before gaps occur and can greatly alter the composition of the advance regeneration layer (Ehrenfeld 1980, Connell 1989, Runkle 1990, Hill 1996, Connell et al. 1997). As this layer represents the template for succession and future forest composition (Brokaw 1985, Marquis et al. 1992, Morin, 1994, George and Bazzaz 1999a), deer and understory plant competitors have the potential to decrease diversity and modify forest successional trajectories (e.g. Rooney et al. 2004).

Deer overbrowsing is arguably the most pervasive factor altering plant diversity in eastern deciduous forests (Rooney et al. 2004). Contemporary deer population levels throughout the eastern United States greatly surpass historical estimates of 3.1 – 4.2 deer/km<sup>2</sup> in more than 50% of all counties east of the Mississippi (Quality Deer Management Association 1999, McShea et al. 1997). Pennsylvania alone has sustained an overabundant deer herd for over 80 years with populations averaging 7.7 – 14.8 deer/km<sup>2</sup> and some localized populations peaking at over 60 deer/km<sup>2</sup> (de Calesta and Stout 1997, Porter 1994). Research examining the impact of deer on plant communities consistently validates the fact that overbrowsing strongly reduces tree species richness, population sizes, and shifts understory composition towards unpalatable or browse-tolerant species (Rooney 2001, Russell et al. 2001, Horsley et al. 2003, Rooney and Waller 2003, Côté et al. 2004, Banta et al. 2005). As a result, the little advanced regeneration that is present is typically restricted to species that are browse tolerant or unpalatable.

Occurring simultaneously with overbrowsing is the aggressive expansion of native and exotic understory herbs or shrubs across vast areas of eastern deciduous forests. Species including rhododendron (*Rhododendron maximum*) and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) cover millions of acres forming nearly impenetrable and monodominant understory canopies and severely interfering with woody regeneration (Monk et al. 1985, McWilliams et al. 1995). Empirical studies suggest the primary mechanism of interference from these herbaceous or shrubby canopies is above-ground competition for light (Horsley 1993a, Beckage et al. 2000, Lei et al. 2002). By intercepting much of the remaining light found in a shaded forest understory, this layer reduces light to very low (< 5% ambient) levels creating conditions at the forest floor that prevent seedling establishment (Nakashizuka 1987, Horsley 1993a, Wada 1993, Walker 1994, Clinton and Vose 1996, George and Bazzaz 1999a, Aubin et al. 2000). In fact, this vegetation stratum can function as a second canopy such that only shade-tolerant species should persist under, and possibly emerge thru an intact understory layer.

In spite of evidence that both deer herbivory and understory plants profoundly alter forest regeneration patterns, researchers and land managers have generally addressed these two factors independently (e.g. Alverson and Waller 1997, Stromayer and Warren 1997, Den Ouden 2000). The key predictions stemming from either approach stipulate that reductions in deer numbers *or* interfering vegetation are key in achieving successful and diverse regeneration (e.g. Marquis et al. 1992). Implementation of management strategies focused on any one factor (e.g. reducing deer impacts *or* removing fern) does not always guarantee successful and diverse regeneration (Marquis 1974, Mladenoff and Stearns 1993, Hill 1996, Schmitz and Sinclair 1997, de la Cretaz and Kelty 2002). We suggest the incongruence between model predictions and empirical field

results may lie in the lack of integration between herbivory and understory plant competition impacts. Indeed, only a handful of experiments simultaneously examined both deer herbivory and understory competition (Horsley and Marquis 1983, Horsley 1993a, Saunders and Puettmann, 1999, de la Cretaz and Kelty 2002). Although valuable in advancing our understanding of herbivore-plant and plant-plant interactions these tests were conducted in fairly bright (15 - 25% full sun), recently thinned forest stands and plantations or simulated deer herbivory on transplanted seedlings via clipping. Therefore, their generality to forest stand dynamics undergoing gap-phase replacement is inconclusive.

In this study, we factorially manipulated deer impact and fern cover in second-growth forests to examine how these two factors, alone and in concert, shape the advance regeneration template. We tested the following three sets of hypotheses. First, if deer overbrowsing limits tree seedling establishment, we predict that 1) overall tree seedling survival and growth should be greater inside exclosures relative to controls, and 2) over time, seedling layer density and richness will be greater inside exclosures as browse intolerant species are afforded protection. Second, if an understory fern stratum operates similarly to an overstory canopy we predict 1) overall tree seedling emergence, survival and growth will increase as fern gap are enlarged, 2) emergence and survival and growth of shade intolerant species should increase with gap size, leading to 3) greater seedling density and richness in fern gaps relative to controls. Finally, eliminating both the overbrowsing and competition constraints should increase seedling density and richness. By contrast, under the dual constraints of herbivory and competition, seedling density and richness will be lowest as species composition shifts towards species that are both shade-tolerant and browse-resistant.



## **4.3 METHODS**

### **4.3.1 Research Sites**

We conducted our study in three 75+ year old sites within the Allegheny High Plateau Region of northwestern Pennsylvania. Two sites, Marienville and Long Run, are owned by Kane Hardwood while the third, Clermont, is managed by Forestry Investment Associates. All sites are representative of the Allegheny Hardwoods forest subtype and experience a cool and humid climate with an average summer temperature of 18.9 °C and an annual precipitation of 109 cm (Lutz 1930, Whitney 1990). The understory is dominated almost exclusively by a dense stratum of hay-scented fern and the midstory layer is virtually absent. This species is impalatable to deer and exhibits aggressive vegetative growth as understory light increases (Cody 1977). Consequently, increased overstory removal coupled with pervasive deer overbrowsing has dramatically increased hay-scented fern cover over the past several decades (de la Cretaz and Kelty 1999, Horsley et al 2003). In the Allegheny region alone, this species historically occupied <1 – 3.3 % of the understory (Lutz 1930) and presently dominates approximately 33% of the forest understory (Royo, unpub. data). Once established, hay-scented fern severely inhibits seedling recruitment and survival (Horsley and Marquis 1983, Drew 1988, Horsley 1993a, George and Bazzaz 1999a,b).

### **4.3.2 Experimental Design**

Our experimental design is a randomized complete block, split-plot design with deer herbivory (Fence) as the main-plot factor and fern gap (Gap) as the within-plot factor. At each of the three sites we established 12 paired (280 m<sup>2</sup>) main plots. In each pair, one main plot was randomly fenced to exclude deer in October 2000 and the other served as an unfenced control. In addition, we established twelve, 2.5 m X 2.5 m (6.25 m<sup>2</sup>) subplots within each main plot and randomly

assigned each subplot one of six levels of fern removal in August 2000 such that each fern removal level (referred hereafter as ‘Gap’) was replicated twice per main plot (Figure 4.1). The removal consisted of glyphosate herbicide application (Accord<sup>tm</sup> and X-77<sup>tm</sup> surfactant) to create the following gap sizes: control (no gap), 1 m<sup>2</sup>, 2.5 m<sup>2</sup>, 3.75 m<sup>2</sup>, 5 m<sup>2</sup> and 6.25 m<sup>2</sup> (i.e. fern removed from the entire subplot). A total of 37 m<sup>2</sup> of area per main plot was treated at the recommended rate for this forest type of 1.15 kg of active ingredient per hectare (Horsley 1981). Embedded in the center of each subplot is a 1 m<sup>2</sup> sampling plot (12 sampling plots/main plot X 12 main plots/site X 3 sites = 432 sampling plots total). All subplots were separated from each other and from the main plot perimeter by a buffer of 1.5 – 2.0 meters.

To obtain recruitment of various species spanning the range of shade tolerance found in this forest type, we augmented woody tree seed availability by direct seeding (Table 4.2). Seeds were added to half of each sampling plot as natural seed fall occurred throughout fall 2000 and spring 2001. The species introduced were the following: black cherry (*Prunus serotina*; 200 seeds/m<sup>2</sup>), red maple (*Acer rubrum*; 600 seeds/m<sup>2</sup>), sugar maple (*Acer saccharum*; 300 seeds/m<sup>2</sup>), black birch (*Betula lenta*; 1700 seeds/m<sup>2</sup>), and white ash (*Fraxinus americana*; 600 seeds/m<sup>2</sup>). Seed was obtained from local sources to prevent the introduction of novel genotypes (Sheffield Seed Supply; Locke, NY & Ernst Conservation Seeds; Meadville, PA). Additionally, we transplanted five sugar maple seedlings (*Acer saccharum* Marsh.) into each control (no gap), 1 m<sup>2</sup>, and 6.25 m<sup>2</sup> fern gap plots. We collected these seedlings from naturally germinating individuals in a sugar maple stand and directly transplanted them in late May 2003.

#### **4.3.3 Sampling Regime**

We monitored seedling emergence, survival, and growth in all plots in summers 2001 thru 2004. Individual seedlings were marked with uniquely numbered plastic binder rings to identify the

specific individual and cohort. For each seedling we collected height, leaf number, and any additional notes (e.g., browsed dieback, etc.). Thus, we have recruitment, by species, for four cohorts, as well as their respective growth and survival data over time.

We measured percent light attenuation at each subplot using an ACCUPAR linear PAR ceptometer (Decagon, Pullman, WA, USA). An additional sensor simultaneously measured full sunlight in nearby openings. Light readings were taken during the growing season (July and August) at dawn and dusk to obtain diffuse light measurements in 2002 and 2004 (Rhoades et al. 2004). We averaged two measurements taken in cardinal directions at each of two heights: 1 m (above fern) and 10 cm (below fern) and calculated total light attenuation as  $\text{PAR below fern} / \text{PAR above overstory canopy}$ .

Finally, we assessed overstory tree composition in 2004 to characterize the canopy at each site. Each tree over 20 cm diameter breast height was identified and measured within each 14 X 20 meter main plot and extending out to include individuals 10 meters from the perimeter of the main plot. This diameter cutoff excludes the smaller trees that do not form part of the canopy and are typically not major seed producers (Marquis et al. 1992).

#### **4.3.4 Statistical Analyses**

For all analyses we averaged the two replicates of each gap size within each main plot prior to analyses. We utilized a mixed model approach where Site and Block and their interactions were considered random factors. We used repeated-measures ANOVA (von Ende 2001) to examine changes in establishment, growth, density, richness (S), diversity (Berger-Parker Index; i.e. the proportional importance of the most abundant species), and the proportion of plots dominated by black cherry (i.e. the proportion of plots in which black cherry represented the tallest stem). Magurran (1988) argued that the Berger-Parker Index coupled with richness (S) provides

interpretable, statistically sound, and ecologically relevant measures of diversity. Further, in forest communities the proportion of plots dominated by a species is a proven predictor of future forest stand composition (Marquis 1979, Tilghman 1989, Ristau and Horsley 1999). In addition, we conducted univariate ANOVA's on seedling survival for each species. We calculated the overall two-year survival as well as first- and second-year survival rates because survivorship during early establishment ( $< 1$  yr) often differs from subsequent years (e.g. Jones et al. 2004). In all analyses data were first assessed for normality and transformed, if necessary, to meet the assumptions of ANOVA. SAS version 9.1 was used for all analyses.

Finally, we projected time to extinction of a cohort ( $< 1$  individual remaining/m<sup>2</sup>) and time to grow above the fern layer (height  $\geq 1.0$  m) in years for black cherry, red maple, pin cherry, and white ash using field data. We calculated time to extinction by multiplying the average recruitment for each species (# seedlings/m<sup>2</sup> at  $t = 0$ ) by its first-year survival to yield the number of seedlings at  $t = 1$ . This value was then multiplied by its second-year survival and iterated yearly ( $t + 1$ ) to provide seedling densities in subsequent years. For each species, we chose the year in which recruitment was greatest as the values for initial cohort recruitment. Similarly, for growth projections we multiplied the average height at emergence by the first year growth rate and subsequently iterated the resulting height by the second year growth rates.

## **4.4 RESULTS**

### **4.4.1 Overstory Composition**

All three sites are typical of the Allegheny hardwood type in which black cherry, red, and sugar maple comprise the majority of canopy trees (Table 4.1). Of the three sites, Clermont has the lowest abundance of black cherry in the canopy (35.4%) while at Long Run and Marienville black cherry represented 68.5% and 55.2% of the individuals  $\geq 14$  cm dbh, respectively.

#### **4.4.2 Efficacy of gap treatments**

Herbicide treatment effectively created six distinct fern gap sizes and increased light availability at 10 cm above-ground. Light availability among gaps  $\geq 2.5\text{m}^2$  was not significantly different ( $P > 0.05$ ) in either year (6.74% – 7.02% full sunlight in 2002 and 7.21% – 7.82% in 2004). Conversely, light availability beneath an intact fern canopy was significantly lower than all other gap treatments in 2002 (4.24% full sunlight;  $P < 0.0001$ ; Tukey pairwise comparison) and significantly lower than gaps  $\geq 2.5\text{m}^2$  in 2004 (3.41 % full sunlight;  $P < 0.0001$ ; Tukey pairwise comparison). The smallest gap size ( $1\text{m}^2$ ) had light levels in between the controls and the larger gaps (5.96% and 4.96% full sunlight in 2002 and 2004, respectively), but did not differ from control plots by 2004 as fern reinvaded the plots ( $P = 0.192$ ; Tukey pair-wise comparison). Given the similarities in light levels among the four larger gap classes and the darker conditions in two smallest gap classes by 2004, we conducted orthogonal contrasts to test for fern effects between fern gap treatments  $\geq 2.5\text{m}^2$  and those  $\leq 1\text{m}^2$ .

#### **4.4.3 Effects of Treatments on Emergence**

Comparisons between the seed augmentation and the non-augmentation in the subplots revealed that seed additions in fall 2000 and spring 2001 did not increase overall emergence ( $F = 0.67$ ,  $P = 0.412$ ). Only white ash exhibited a recruitment pulse from seed additions in 2002 with emergence occurring exclusively on the augmented side ( $F = 223.1$ ,  $P < 0.0001$ ). Due to the general lack of a seed augmentation effect, this treatment was excluded from all subsequent analyses.

Overall, emergence among species varied greatly over time (Table 4.3, Figure 4.2). Black cherry emergence significantly decreased following a mast event in the fall of 2000 with spring emergence in 2001 being an order of magnitude greater in 2001 than in 2004 (Figure

4.2a). Black cherry emergence was significantly greater in control plots relative to fenced plots and was unaffected by openings in the fern canopy (Table 4.3a, Figure 4.2a). Red maple emergence increased significantly over time (Table 4.3a) and the significant Site term indicated that much of this increase was driven by one site (Clermont) which had the high number of germinating individuals following a mast year in 2004. Red maple emergence had a tendency to increase within gaps relative to non-gaps ( $F = 3.98$ ,  $P = 0.074$ , Figure 4.2b). Pin cherry emergence also increased over time with the highest emergence in 2003 and 2004, with a significant Site term indicating particularly high emergence at Long Run. Fern gaps significantly increased the emergence of pin cherry (Table 4.3a, Figure 4.2c). Birch exhibited appreciable emergence only in 2004 and its emergence was significantly enhanced in fern gap plots (Table 4.3a, Figure 4.2d).

#### **4.4.4 Effects on Survival**

Overall survivorship was greatest for black cherry followed by red maple, pin cherry and white ash (Figure 4.3). Protection from deer browsing did not increase the survival of any of the species relative to control plots (Table 4.4). Creating gaps in the fern canopy significantly increased the survivorship both the first and second year survival for black cherry and red maple. Gaps also significantly increased the first year survival and marginally increased ( $P = 0.054$ ) the second year survival of pin cherry. White ash had uniformly low survivorship across all treatment areas (approx. 12%), however it did exhibit higher survival within the fences in its second growing season.

#### **4.4.5 Effects on Height Growth**

Overall increases in seedling height were slight over time. Neither protection from deer herbivory nor creation of fern gap significantly affected height for any tree species (Table 4.3b).

Over four years we did not observe a single tree seedling growing through the fern in either the fenced or in control plots.

#### **4.4.6 Projections on cohort extinction and growth**

Beneath an intact fern canopy, no species was projected to have sufficient survival to grow tall enough to escape the fern stratum (Table 4.6). Further, even with the creation of a gap in the fern canopy, we found projected only black cherry would have a chance at overtopping the fern canopy (Table 4.6).

#### **4.4.7 Seedling layer composition and diversity**

Species richness increased over time across all treatments, however there was a greater rate of increase in fern gaps relative to control plots as evidenced by the significant Gap\*Year interaction (Table 4.5, Figure 4.4a). Species richness increased from 1.46 species/m<sup>2</sup> in 2001 to 2.65 species/m<sup>2</sup> by 2004 (67% increase) compared to an average across all gaps of 1.61 species/m<sup>2</sup> in 2001 to 3.57 species/m<sup>2</sup> by 2004 (120% increase). Seedling density increased significantly over time, yet the rate of increase was greater in gaps than controls. Seedling densities in fern gaps  $\geq 2.5$  m<sup>2</sup> increased by over 100% compared to controls while in fern covered plots density remained relatively unchanged over time (Figure 4.4b). Protection from deer herbivory did not significantly change overall seedling density over time, however, control plots consistently had significantly higher seedling density than the fenced plots. Species diversity as expressed by the Berger Parker Index (1/d) increased similarly across all treatments (Table 4.5; Figure 4.4c). Finally, although the proportion of plots dominated by black cherry declined over time there were no significant effects from fencing or creating fern gaps (Table 4.5; Figure 4.4d). In fact, even by year 4 this single species retained dominance of > 60% of all plots across all sites.

## **4.5 DISCUSSION**

### **4.5.1 Seedling layer response to deer herbivory**

Despite the preponderance of data indicating that deer overbrowsing strongly limits tree seedling composition in forest understories, our results do not provide strong evidence for this factor. However, we do not interpret this to mean deer herbivory is unimportant in our system. In fact, ample evidence exists from within the region substantiating impacts of chronic deer overbrowsing on the plant community (Hough 1949, Webb et al. 1956, Marquis 1981, Rooney and Dress 1997, Horsley et al. 2003, Banta et al. 2005, Latham et al. 2005). We suggest that the lack of an effect may arise from a variety of methodological and biological reasons. First, inherent in the split plot experimental design is a loss of power to detect differences in the whole plot effect, in this case, deer herbivory (Steel and Torrie 1980, Sokal and Rohlf 1995). Second, deer preferentially browse seedlings and saplings in larger size classes (Horsley and Marquis 1983) and the vast majority of censused individuals were less than 15 cm tall. Third, the overwhelming majority of seedlings were black cherry, a highly unpalatable species (Healy 1971, Latham et al. 2005). Fourth, it is possible that deer cannot “see” the seedlings as they are overtopped by a canopy of fern for the majority of the growing season (e.g. Horsley and Marquis 1983, De Steven 1991, Saunders and Puettmann 1999, Peterson and Pickett 2000). Finally, our sites are embedded within a forest matrix that is dominated by the unpalatable, hay-scented fern (Healy 1971). Although we consistently found evidence of deer (e.g. hoof prints, scat, fawn beds), it is probable that deer only lightly utilize these areas opting to forage in areas with higher preferred food abundance, including forest edges, agricultural fields, and newly cut stands (e.g. Palmer et al. 2003).

Alternatively, deer may have no discernable impact on the system because the plant community has collapsed to an alternative, ‘degraded’ state in which the dynamics are no longer



driven by herbivory, but rather, are governed by competition from the dense and widespread carpet of unpalatable hay-scented fern (Schmitz and Sinclair 2004, Suding et al. 2004). The existence of abrupt shifts in plant communities states within a site has long been recognized (reviewed by Young et al. 2001), and modeled, particularly for grazing systems (e.g. “State-Transition” models; Westoby et al. 1989, Laycock 1991, Schmitz and Sinclair 1997). In fact, others have called hay-scented fern areas within the Allegheny Plateau ‘self-perpetuating climax communities’ and ‘alternate stable states’ (Horsley and Marquis 1983, Schmitz and Sinclair 1997, Stromayer and Warren 1997). Such a shift could occur in a forests originally containing diverse, abundant, and palatable woody regeneration when overbrowsing beyond a particular threshold point forces a collapse to a new state dominated by unpalatable plant species (Figure 4.5). Once at this new state, subsequent reductions in herbivore pressure may allow a very slow return to the original, diverse plant community state or no return at all (Suding et al. 2004). This scenario reveals a complex, yet temporally separated interaction between deer overbrowsing and fern cover. Deer overbrowsing is a primary factor in the collapse of woody regeneration and the concomitant increase in unpalatable fern cover (Horsley and Marquis 1983, de la Cretaz and Kelty 1999, Banta et al. 2005). Following the monopolization of the understory by fern, however, this newly established understory canopy independently limits regeneration (Royo, Chapter 2).

#### **4.5.2 Seedling layer response to fern gaps**

We found that a fern canopy strongly limited the abundance and composition of the seedling layer. Furthermore, we found non-significant Gap\*Site interactions in 14 out of 17 tests on various establishment and diversity measures. This consistency across three widely separated sites representative of much of the forested area in the region reveals the strength and

predictability of fern cover as a regeneration barrier. Furthermore, our experimental sites are characteristic of many forests worldwide containing widespread, nearly monodominant understory layers (Royo, Chapter 2). Thus, our work suggests these layers represent strong barriers to regeneration can limit tree seedling diversity globally.

Seedling richness and density doubled in plots with fern gaps (Figure 4.4 a,b). The overall increase over time was partly a result of a red maple mast crop in 2004. In fact, red maple emergence averaged less than 1 individual/m<sup>2</sup> in 2001 and increased by up to two orders of magnitude in subsequent years. Nonetheless, our results indicate that the establishment of additional species, particularly within fern gaps, is partly responsible for this pattern. Similarly, Drew (1988) reported on increases in diversity, as measured by the Shannon Index ( $H'$ ), in fern-free plots relative to fern-covered plots in thinned Allegheny hardwood stand in New York, although his results include both woody and herbaceous plants. Moreover, similar relationships between hay-scented fern and inhibition of tree regeneration documented throughout the northeastern U.S. and Canada substantiate the fact that the generality of this phenomenon extends beyond the Allegheny Plateau (e.g. Cody et al. 1977, de la Cretaz and Kelty 1999, George and Bazazz 1999 a, b, Hill 2001)

Our results also suggest that gaps in the fern canopy affect the seedling layer in much the same way as do overstory gaps. Emergence and survival of several shade intolerant and intermediately tolerant tree species (e.g. pin cherry, birch, red maple) increased in both our study and studies investigating understory responses following overstory gap formation (e.g. Clinton et al. 1994, Beckage et al. 2000, Peterson and Pickett 2000, Prévost and Pothier 2002). Other shade intolerant species (e.g. *Rubus* spp.) also increased within fern gaps, but restricted sample sizes precluded any analyses. In contrast, the emergence of black cherry and white ash, two other

shade intolerant species, was unaffected by fern gaps. Similarly, Kolb and others (1990) found inconsistent increases in black cherry emergence following fern gap creation (only 2 of 4 years) while George and Bazzaz (1999a) found no effect of fern gaps on white ash emergence. Both black cherry and white ash germinate early in the spring (Marquis 1973, Horsley 1993a, George and Bazzaz 1999a) prior to fern canopy establishment and subsequent light reduction (Hill 1996). This spring emergence phenology may allow these species to circumvent any restriction on emergence by fern cover (e.g. de la Cretaz and Keltz 2002).

Fern canopy gaps increased the survivorship of black cherry, red maple and pin cherry, but not white ash. All of these species are ranked as shade intolerant and intermediately tolerant and thus, gaps should increase their survival. Mortality of white ash, averaged across treatments, was the highest among all species (87%) and possibly masked any effect of fern gap creation. This species may be so intolerant that even in fern gaps it cannot persist beneath a closed overstory canopy (see Pacala et al. 1996). Alternatively, the low survivorship of white ash may be due to its sensitivity to soil calcium deficiencies (Erdmann et al. 1979), a condition common in unglaciated Allegheny plateau-top sites such as ours (Bailey et al. 2004).

Height was entirely unaffected by fern gap creation, whereas overstory gaps typically enhance seedling height (e.g. Marquis 1973, Hannah 1993, Wayne and Bazzaz 1993, Sipe and Bazzaz 1995). The discrepancy between the establishment parameters (emergence and survival) and growth suggests that light beneath a closed overstory remains limiting for seedling growth despite the creation of fern gaps (e.g. Pacala et al. 1994, Finzi and Canham 2000). Seedling growth is typically less sensitive to small increases in light than emergence and survival (Kobe et al. 1995, Chen 1997, Beckage and Clark 2005). Furthermore, most of the species surveyed rank as relatively shade intolerant and therefore should not exhibit marked increases in growth

beneath a closed overstory canopy (Hough 1936, Marquis 1979). Our projections of survival in the seedling bank vs. time needed to overtop the fern suggest that even without a fern canopy only black cherry may enter the 1 meter size class prior to extinction of the cohort (Table 4.6). We believe these projections likely underestimate the likelihood of successful establishment into the sapling layer. First, our chosen initial values for emergence were based on the highest emergence rate observed across all four years. This increased fecundity, in effect, raises cohort survival by partially offsetting mortality and growth disadvantages (Beckage and Clark 2003). Furthermore, although our data indicated no deer impact on small seedlings, survival and growth probabilities would likely decrease as seedlings grew taller and were more frequently browsed. Consequently, we believe any increase in species richness gained by creating fern gaps will be transient as cohorts that establish under a closed canopy and high deer browsing will likely never overtop the fern stratum (Hill 1996, George and Bazzaz 1999b, de la Cretaz and Kelty 2002).

#### **4.5.3 Have Allegheny Forests embarked on a “March towards Monodominance”?**

In spite of the increases in density and richness following fern gap creation, after four years the seedling layer remained heavily dominated by one species - black cherry. The relative abundance of black cherry ranged from over 90% in all three sites in summer 2001 to 35% – 70% by 2004 following several poor black cherry seed years and masting events of red maple. Nonetheless, even at the lowest point, the relative abundance of black cherry seedlings equaled or exceeded its relative abundance in the overstory, suggesting a continuing momentum towards dominance by cherry. This interpretation is further strengthened by our measure of percent of plots dominated by black cherry which similarly indicated that by the fourth year black cherry retained dominance in > 60% of the plots and that neither deer exclusion nor creation of gaps in the fern canopy significantly altered this pattern. Our results are consistent with Horsley et al.

(2003) who in a 10 year experiment found that black cherry retained its dominance in uncut stands with low deer and greatly increased in dominance in areas with high deer.

There is empirical evidence corroborating the claim of increasing black cherry dominance in the Allegheny region. Historically, this species formed less than 1% of the overstory trees in pre-settlement forests (Whitney 1990); however, it presently forms approximately 25% of the individuals in most second growth forests and nearly 50% of the individuals in third growth forests (Whitney 1990, Allegheny National Forest 1995, Morin et al. 2001). We believe that this increase over time is a direct legacy of deer overbrowsing (Marquis 1989) which has now set the stage for persistent and even increasing dominance. This interpretation not only is supported by our data, but also bolstered by an experiment in the region examining vegetation patterns under varying deer densities (Horsley et al. 2003). In this work, the authors demonstrated that black cherry abundance increased linearly with deer density, regardless of management history (e.g. clear-cut and uncut stands). The authors further concluded that despite slight increases in the abundance of other species, black cherry ‘sustained’ its dominant position even after 10 years of low deer density (Horsley et al. 2003).

#### **4.5.4 Traits conferring an advantage to black cherry in contemporary forests**

Once established as the dominant component of the overstory, black cherry possesses a number of traits that enable it to successfully establish in contemporary forests. Among the species common to the region, black cherry has a higher seed crop frequency (every 1 – 3 years; Bjorkbom 1979, Horsley et al. 1994), a higher seed viability (85 - 91% of seeds viable; Marquis 1973, Bjorkbom 1979), and a long-lived seed bank (3 – 5 years; Wendel 1972, Marquis 1975) relative to many of its competitors. Additionally, its early emergence relative to fern canopy establishment allows it to circumvent the fern’s negative effect on germination unlike several of

its competitors (e.g. red maple, pin cherry, birch; Table 4.3a). Furthermore, black cherry is unpreferred by deer, and is often the last species in northern hardwood forests consumed by deer (Healy 1971, Horsley et al. 2003, Latham et al. 2005). Finally, black cherry's growth and recovery from defoliations is less affected by reduced soil base cation availability than other associated species (e.g. sugar maple; Long et al 1997). This suggests that the potential decreases in tree growth and survivorship resulting from acid deposition induced nutrient changes will be less severe on black cherry relative to other associated species (Bailey et al. 2005).

Although classified as a relatively shade intolerant species, we found the early survival of black cherry more closely resembles a shade tolerant species. The average survivorship over two years of black cherry was the greatest among all seedlings including the traditionally shade tolerant red maple (Table 4.2; Figure 4.3). Other studies have similarly concluded that black cherry saplings have the ability to outgrow many other tree species at both high and low light (e.g. Pacala et al. 1996). Nonetheless, we do not suggest that black cherry be reclassified as a shade tolerant species whose individuals can survive and consistently grow over long periods of time underneath a closed canopy (*sensu* Canham 1989) as we did not observe any individuals emerging thru the fern into sapling size class (see also Hill 1996). We do, however, emphasize that its high seed availability, viability, and seed banking ability coupled with its relatively high seedling survival and impalatability to deer allow it to consistently represent the dominant species in the seedling bank, both in terms of density and height in Allegheny hardwood forests. Consequently, black cherry's 'meteoric' increase in abundance (Whitney 1990) over the past 100 years is partly a result of this species being the only one poised to capitalize on overstory gaps.

#### **4.5.5 Management Implications**

Nearly a century of deer overabundance in the Allegheny region has resulted in a floristically impoverished forest dominated by unpalatable plant species, namely hay-scented fern in the understory and black cherry in the overstory. This study suggests that, left unmanaged, long-term forest dynamics in the Allegheny Plateau will mirror the pattern of increasingly depauperate forests across much of the eastern U.S. (White and Mladenoff 1994, Foster et al. 1998, Fuller et al. 1998, Rooney et al. 2004). Consequently, we suggest that forest management not only is useful, but perhaps indispensable, in order to curb the trend towards increasing monodominance.

Our results demonstrate that managing light availability at the forest floor is vital in order to initially augment seedling layer diversity. By eliminating the deeply shaded conditions (< 5% ambient) attributable to fern cover, we significantly increased seedling layer density and richness as species other than black cherry established in the understory. Nonetheless, we suspect this increase is merely ephemeral as most individuals belong to shade intolerant and intermediately tolerant species that will not persist and grow in the dark conditions (5 – 10% ambient) found beneath an intact overstory (Marquis 1979, Pacala et al. 1994, Finzi and Canham 2000). Given these light limitations, we suggest the following treatments could stem the tide of increasing monodominance. First, our results indicate that eliminating the low canopy provides an establishment window for other species. Second, as this increase is likely short-lived, we suggest utilizing a moderate overstory removal (e.g. shelterwood cut) cut to increase light at the soil surface to overcome the growth and survival limitation imposed by an intact overstory canopy (Hannah 1988, Nyland 2002). Third, we recommend timing any overstory removal to coincide with a period of relatively diverse understory conditions (see also Marquis 1979, Horsley 1982, Marquis et al. 1992). For example, our study suggests that a canopy disturbance

in 2001 would result in a less diverse successional trajectory (95% of plots dominated by cherry; Figure 4.4d) compared to a disturbance in 2004 when cherry dominated an average of 72% of the plots. Finally, despite not detecting a deer effect or a deer\*gap interaction on the small seedlings censused this study, a wealth of alternative evidence demonstrates that diverse and successful regeneration ultimately hinges on managing deer impacts (reviewed by McShea et al. 1997, Russell et al. 2001, Côte et al. 2004, Latham et al. 2005). This can be accomplished either directly via fencing and hunting or indirectly by diluting browsing impacts across a heterogeneous landscape containing abundant forage patches (e.g. Jandl et al. 2002, Augustine and De Calesta 2003, Gordon et al. 2004).

North American eastern deciduous forests confront an ever escalating array of novel stressors to canopy health (e.g. Beech Bark Disease, Hemlock Woolly Adelgid) that increase tree mortality and ultimately influence canopy gap dynamics (Kransy and Whitmore 1992, Kransy and DiGregorio 2001, Orwig et al. 2002). Given the current understory regeneration template dominated by unpalatable plant species and a continued deer overabundance, forests in the Allegheny region are poised to move towards even greater homogeneity. Left unchecked, these threats and their ensuing impacts may compel ecologists and land managers to employ heroic efforts across broad portions of the landscape in order to sustain forest diversity.



**Table 4.1 Overstory Composition**

Relative abundance (%) of individuals  $\geq 20$  cm diameter at breast height at each of the three sites.

	<b>Marienville</b>	<b>Long Run</b>	<b>Clermont</b>
Black Cherry	55.2	68.5	35.4
Red Maple	43.2	29.5	29
Sugar Maple	< 1.0	1.4	32.5
Striped Maple	-	-	< 1.0
White Ash	< 1.0	-	-
Cucumber Tree	< 1.0	-	-
American Beech	-	< 1.0	2.9
Birches	-	< 1.0	-

**Table 4.2 Shade tolerance rankings.**

Shade tolerance rankings for species found within our study collated after a) Burns and Honkala (1990), or b) mortality at 1% ambient light where 1 reflects lowest tolerance and 5 reflects greatest (Kobe et al. 1990).

<b>Species</b>	<b>Shade tolerance<sup>a</sup></b>	<b>Shade tolerance<sup>b</sup></b>
<i>Prunus pensylvanica</i>	Very Intolerant	-
<i>Fraxinus americana</i>	Intolerant	1
<i>Prunus serotina</i>	Intolerant	3
<i>Betula nigra</i>	Intolerant	-
<i>Betula allegheniensis</i>	Intermediate	4
<i>Acer rubrum</i>	Tolerant	2
<i>Acer saccharum</i>	Very Tolerant	5

**Table 4.3 MANOVA results on germination and growth.**

Multivariate repeated measures analysis of variance applied to A) germination and B) height growth. Dashed line (-) indicates that i) repeated measures was impossible due to only one year of data (White Ash and Birches), or ii) test was not possible due to low sample size.

**(A) Germination**

Source of Variation	Black Cherry Germination			Red Maple Germination			Pin Cherry Germination			White Ash Germination			Birch Germination		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Site	2, 15	3.66	0.051	2, 15	6.88	0.0076	2, 15	6.8	0.008	2, 15	2.13	0.153	2, 15	1.91	0.183
Fence	1, 2	22.62	0.042	1, 2	6.87	0.119	1, 2	1.62	0.33	1, 2	0.55	0.536	1, 2	2.69	0.242
Fence*Site	2, 15	0.16	0.857	2, 8	0.4	0.679	2, 15	2.16	0.149	2, 15	0.55	0.536	2, 15	2.5	0.116
Gap	5, 10	1.00	0.462	5, 10	2.86	0.074	5, 10	3.56	0.041	5, 10	0.29	0.905	5, 10	4.45	0.022
Gap*Site	10, 75	0.90	0.535	10, 75	1.86	0.064	10, 75	3.56	0.0007	10, 75	2.71	0.007	10, 75	1.42	0.189
Fence*Gap	5, 85	0.81	0.547	5, 85	0.88	0.495	5, 85	0.25	0.939	5, 85	0.91	0.479	5, 85	0.77	0.575
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	0.10	0.762	1, 10	3.98	0.074	1, 10	13.11	0.005	1, 10	0	0.998	1, 10	18.41	0.002
Year	3, 255	930.32	<0.0001	2, 42	1026.44	<0.0001	2, 170	25.8	<0.0001	-	-	-	-	-	-
Fence*Year	3, 6	5.66	0.035	2, 6	3.2	0.105	2, 4	0.76	0.526	-	-	-	-	-	-
Gap*Year	15, 30	2.79	0.008	10, 30	1.15	0.357	10, 20	1.32	0.284	-	-	-	-	-	-

**(B) Height Growth**

Source of Variation	Black Cherry Growth			Red Maple Growth			Sugar Maple Growth			White Ash Growth			Birch Growth		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Site	2, 15	6.5	0.0093	2, 15	3.09	0.0752	2, 15	1.52	0.251	-	-	-	-	-	-
Fence	1, 2	13.61	0.066	1, 2	0.12	0.759	1, 2	0	0.972	-	-	-	-	-	-
Fence*Site	2, 15	0.1	0.905	2, 8	1.32	0.319	2, 15	0.91	0.424	-	-	-	-	-	-
Gap	5, 10	0.44	0.814	5, 10	1.78	0.204	2, 10	0.53	0.62	-	-	-	-	-	-
Gap*Site	10, 75	3.05	0.003	10, 43	0.68	0.738	4, 30	0.89	0.483	-	-	-	-	-	-
Fence*Gap	5, 74	1.84	0.115	5, 21	0.44	0.817	2, 26	2.86	0.076	-	-	-	-	-	-
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	0.19	0.669	-	-	-	1, 10	0.13	0.738	-	-	-	-	-	-
Year	3, 255	913.79	<0.0001	2, 42	69.57	<0.0001	1, 26	43.27	<0.0001	-	-	-	-	-	-
Fence*Year	3, 6	1.74	0.257	2, 4	0.21	0.817	1, 2	0.72	0.486	-	-	-	-	-	-
Gap*Year	15, 30	0.93	0.547	10, 20	1.75	0.139	2, 4	0.14	0.877	-	-	-	-	-	-

**Table 4.4 ANOVA table on seedling survival.**

A) Average survival over two growing season (2002 – 2004), B) survival following one growing season (2002 – 2003), C) Survival of the second growing season (2003 – 2004). Sugar maple analysis represents survival of transplanted seedlings from 2003 – 2004.

**(A) Average**

Source of Variation	Black Cherry Survival			Red Maple Survival			Pin Cherry Survival			White Ash Survival			Sugar Maple Survival		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Site	2, 15	2.28	0.137	2, 15	4.38	0.032	2, 15	1.55	0.245	2, 15	2.74	0.097	2, 15	8.26	0.004
Fence	1, 2	1.17	0.392	1, 2	0	0.952	1, 2	0.17	0.722	1, 2	5.74	0.139	1, 2	0.05	0.846
Fence*Site	2, 15	0.66	0.53	2, 15	0.57	0.579	2, 15	0.65	0.534	2, 15	0.12	0.887	2, 15	1.14	0.345
Gap	5, 10	11	<0.001	5, 10	5.09	0.014	5, 10	2.12	0.146	5, 10	0.86	0.537	2, 10	3.84	0.117
Gap*Site	10, 75	1.83	0.07	10, 75	0.98	0.468	10, 75	1.18	0.319	10, 75	1.64	0.111	4, 30	1.01	0.419
Fence*Gap	8, 85	0.44	0.821	8, 85	1.01	0.419	8, 85	0.26	0.932	8, 85	1.52	0.192	2, 34	0.90	0.416
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	32.32	<0.001	1, 10	14.47	0.004	1, 10	3.76	0.081	1, 10	0	0.998	1, 10	0.13	0.738

**(B) First Growing Season**

Source of Variation	Black Cherry Survival			Red Maple Survival			Pin Cherry Survival			White Ash Survival		
	df	F	P	df	F	P	df	F	P	df	F	P
Site	2, 15	3.14	0.073	2, 15	8.87	0.003	2, 15	3.26	0.067	2, 15	2.89	0.087
Fence	1, 2	0.47	0.565	1, 2	2.08	0.286	1, 2	0.33	0.624	1, 2	0.42	0.584
Fence*Site	2, 15	0.39	0.686	2, 15	0.14	0.874	2, 15	1.84	0.193	2, 15	0.78	0.477
Gap	5, 10	19.57	<0.0001	5, 10	3.98	0.03	5, 10	2.86	0.074	5, 10	0.94	0.496
Gap*Site	10, 75	0.47	0.905	10, 75	1.05	0.412	10, 75	1.05	0.415	10, 75	2.39	0.016
Fence*Gap	8, 85	0.78	0.568	8, 85	0.82	0.537	8, 85	0.20	0.963	8, 85	0.51	0.771
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	1.36	<0.0001	1, 10	11.72	0.007	1, 10	10.33	0.009	1, 10	2.18	0.171

**(C) Second Growing Season**

Source of Variation	Black Cherry Survival			Red Maple Survival			Pin Cherry Survival			White Ash Survival		
	df	F	P	df	F	P	df	F	P	df	F	P
Site	2, 15	0.7	0.512	2, 15	4.82	0.024	2, 15	3.41	0.06	2, 15	3.35	0.063
Fence	1, 2	0.4	0.592	1, 2	0.05	0.839	1, 2	0.45	0.571	1, 2	341.12	0.0029
Fence*Site	2, 15	1.64	0.227	2, 15	0.68	0.52	2, 15	0.68	0.519	2, 15	0.01	0.99
Gap	5, 10	9.43	0.002	5, 10	3.87	0.033	5, 10	2.09	0.15	5, 10	0.73	0.614
Gap*Site	10, 75	1	0.449	10, 75	0.99	0.462	10, 75	1.09	0.379	10, 75	1.12	0.359
Fence*Gap	8, 85	1.47	0.209	8, 85	1.28	0.282	8, 85	0.35	0.879	8, 85	1.01	0.417
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	21.63	<0.001	1, 10	10.98	0.008	1, 10	4.76	0.054	1, 10	0.11	0.742

**Table 4.5 MANOVA table on community-level parameters.**

Multivariate repeated measures analysis of variance applied to species richness, total density (# individuals/m<sup>2</sup>), Berger-Parker (1/d), and the proportion of plots dominated by black cherry.

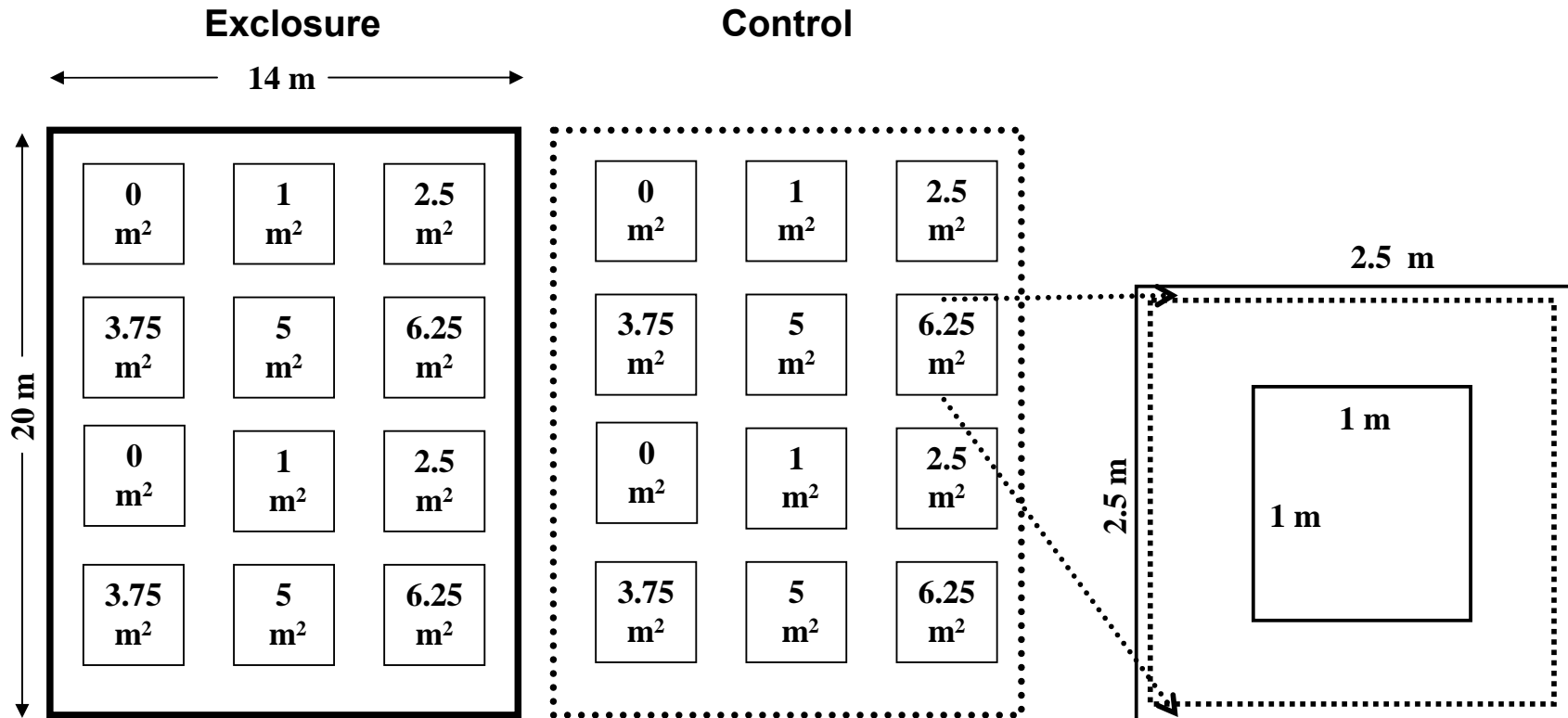
Source of Variation	Richness			Density			Berger Parker (1/d)			Proportion of Plots Do by Black Cherr	
	df	F	P	df	F	P	df	F	P	df	F
Site	2, 15	1.56	0.242	2, 15	0.59	0.565	2, 15	4.03	0.039	2, 15	0.82
Fence	1, 2	9.94	0.087	1, 2	54.19	0.018	1, 2	0.82	0.461	1, 2	6.37
Fence*Site	2, 15	0.03	0.974	2, 15	0.05	0.953	2, 15	0.66	0.529	2, 15	0.67
Gap	5, 10	8.38	0.002	5, 10	9	<0.001	5, 10	0.82	0.565	5, 10	1.94
Gap*Site	10, 75	1.18	0.319	10, 75	0.88	0.558	10, 75	1.01	0.440	10, 75	1.4
Fence*Gap	8, 85	1.93	0.098	8, 85	0.14	0.983	5, 82	0.3	0.913	5, 84	1.42
= 2.5 m <sup>2</sup> vs = 1.0 m <sup>2</sup> Gaps	1, 10	23.55	<0.001	1, 10	29.47	<0.001	1, 10	0.02	0.894	1, 10	1.37
Year	3, 255	537.53	<0.0001	3, 255	281.81	<0.0001	3, 246	423.89	<0.0001	3, 252	2.89
Fence*Year	3, 6	0.94	0.476	3, 6	1.14	0.407	3, 6	1.62	0.163	3, 6	2.33
Gap*Year	15, 30	2.45	0.017	15, 30	4.18	<0.001	15, 30	0.92	0.554	15, 30	0.99

**Table 4.6 Projections times (years) on cohort extinction and growth to 1 meter.**

<b>Species</b>	<b>Time to Cohort Extinction</b>		<b>Time to 1 meter</b>	
	<b>Fern</b>	<b>Gap</b>	<b>Fern</b>	<b>Gap</b>
<i>Prunus serotina</i>	10	18	13	12
<i>Acer rubrum</i>	5	9	28	16
<i>Prunus pensylvanica</i>	<1	3	*	6
<i>Fraxinus americana</i>	2	2	75	20

**Figure 4.1 Schematic of split plot experimental design.**

Whole plot factor is deer manipulations (solid line = exclosure, dashed line = control). Split plot factor of fern gap creation is applied randomly to each of 12 subplots within a main plot. Each fern gap opening ( $\text{m}^2$ ) is represented twice within each main plot. Seedling monitoring was restricted to the center  $1 \text{ m}^2$  area.

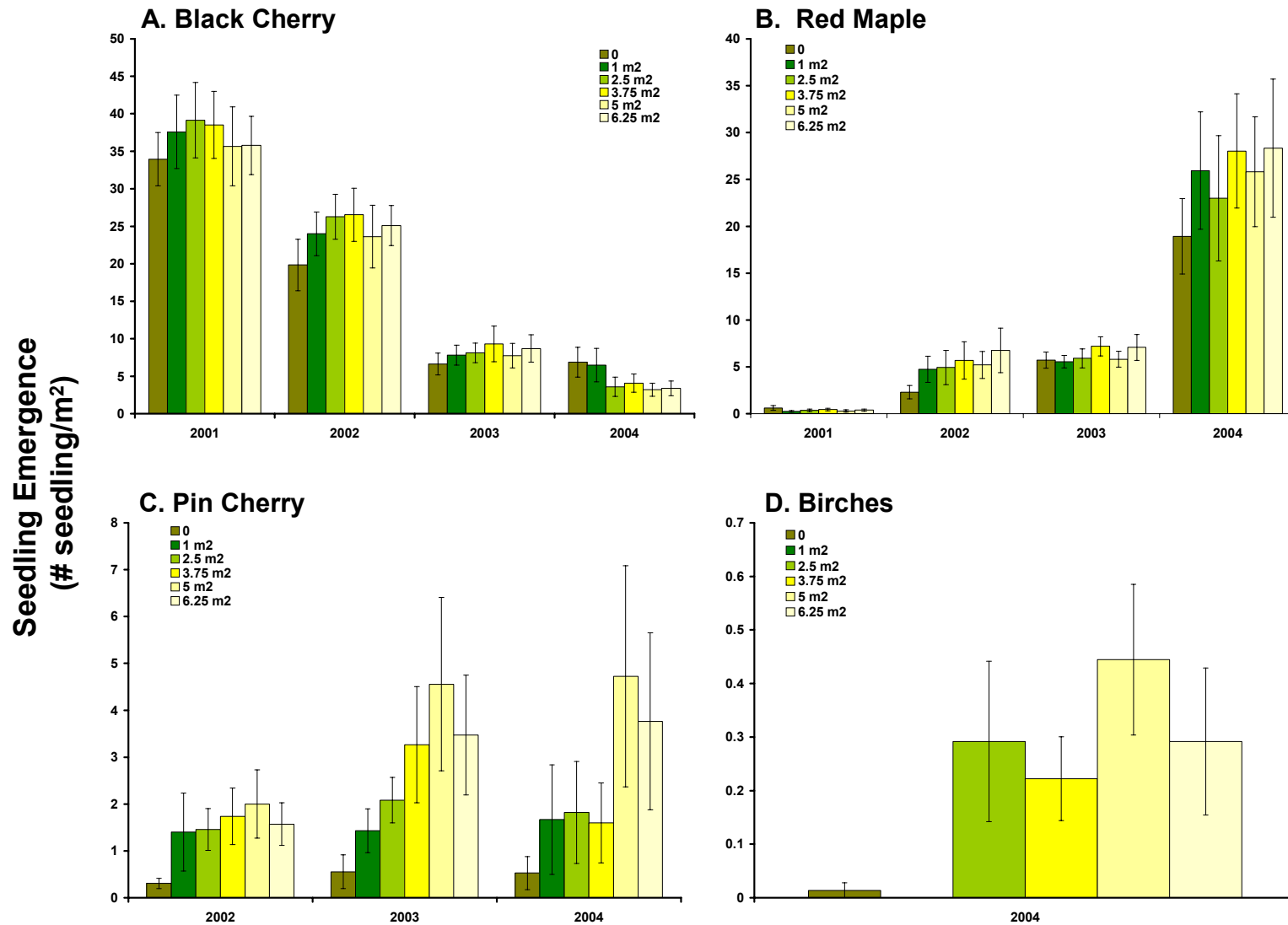


6 Blocks per site \* 3 sites = 18 blocks

24,  $1 \text{ m}^2$  sampling plots/block \* 18 blocks = 432 sampling plots

**Figure 4.2 Seedling emergence over time.**

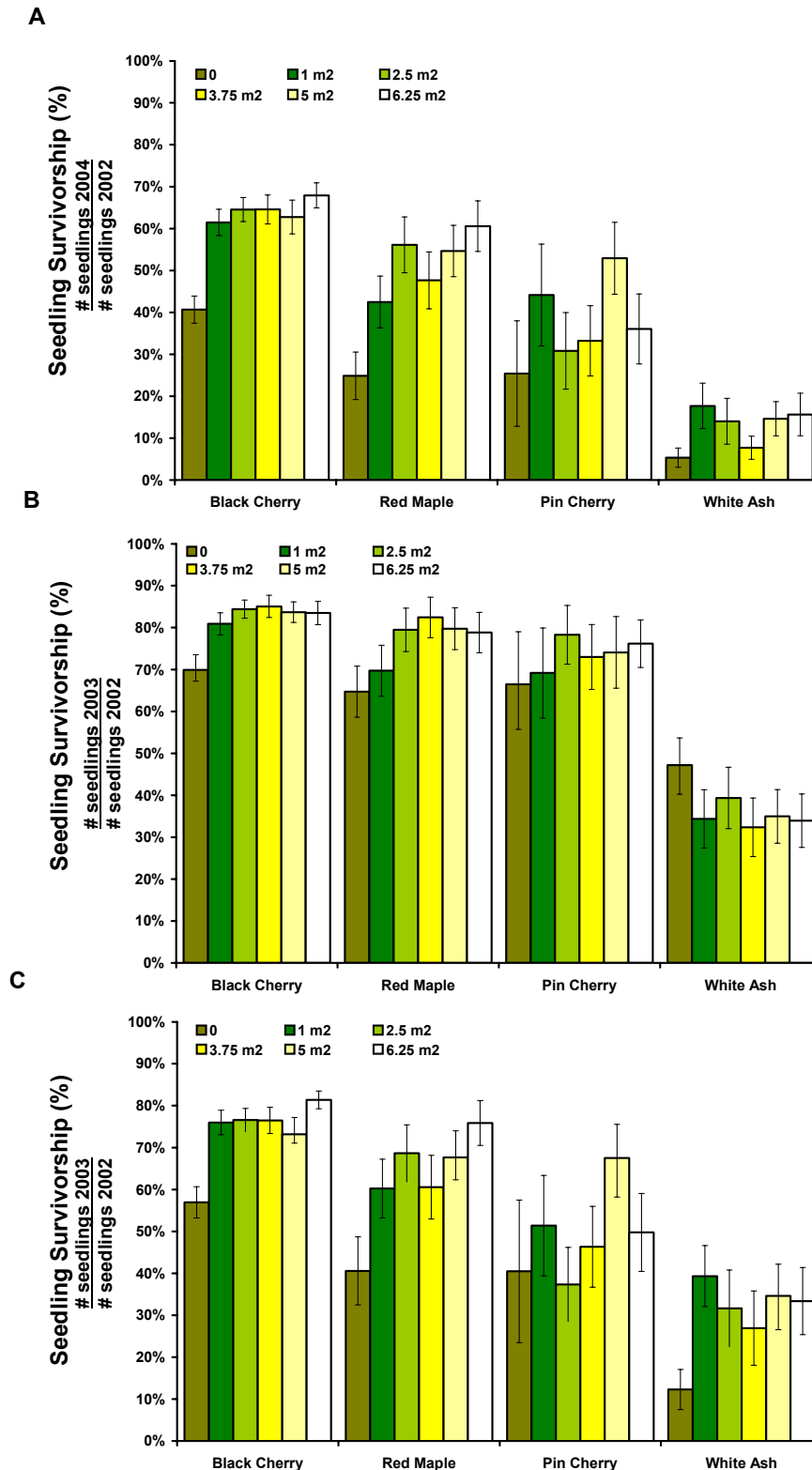
A) Black Cherry, B) Red Maple, C) Pin Cherry, D) Birches. Black cherry and red maple had measurable germination across all sites in all four years. Pin cherry only had appreciable germination in 2002 – 2004 while the Birches only had noticeable germination in 2004.





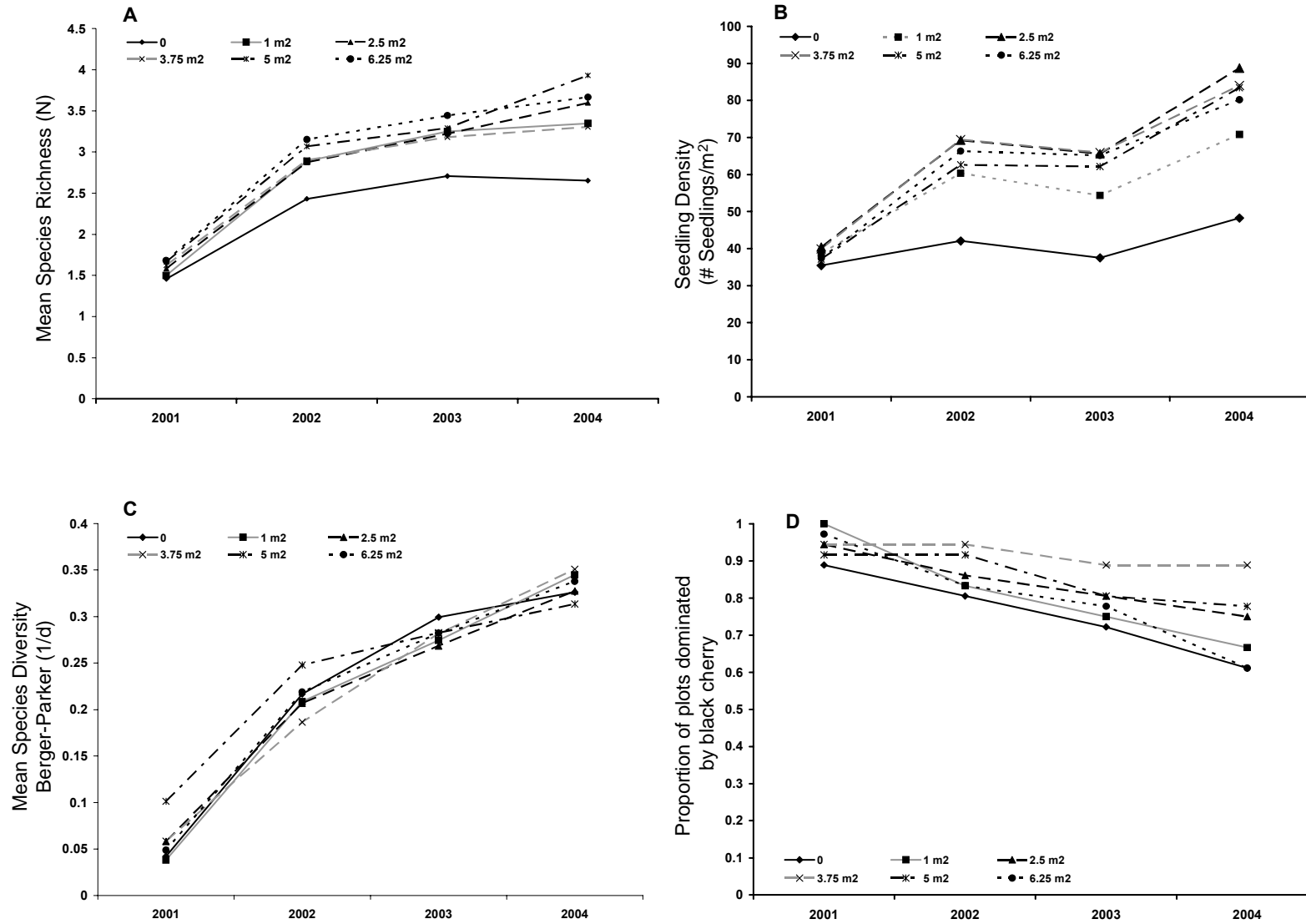
**Figure 4.3 Seedling survival of 2002 cohort.**

A) Average across two growing seasons (2002 – 2004), B) First growing season (2002 – 2003), and C) Second growing season (2003 – 2004).



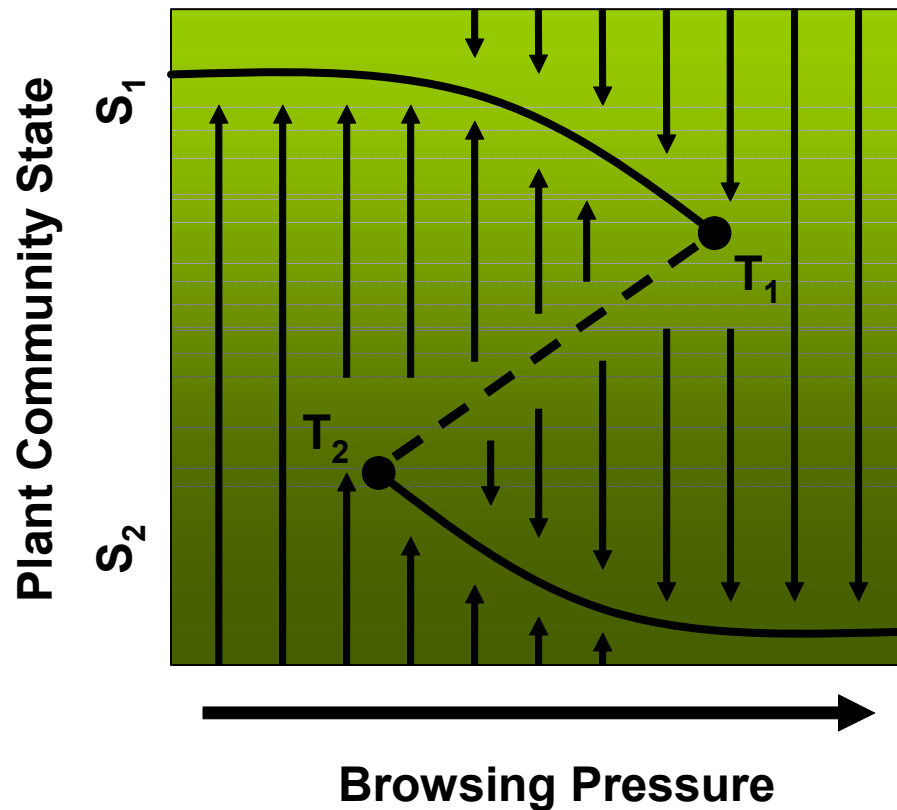
**Figure 4.4 Changes in community level parameters over time.**

A) Species Richness (N), B) Seedling Density (# individuals/m<sup>2</sup>), C) Species Diversity as expressed by the Berger-Parker Index (1/d), and D) Proportion of plots dominated by black cherry.



**Figure 4.5 State-Transition model.**

Graphical model representing abrupt shifts between plant community states (modified from Suding et al. 2004). In  $S_1$ , a diverse woody understory community persists under a wide range of deer browsing pressures. However, if browsing exceeds threshold  $T_1$ , then the community rapidly collapses to a fern-dominated understory community ( $S_2$ ). Return to  $S_1$  may only be possible with prolonged low browsing below threshold point  $T_2$  or with active management to mitigate the influence of fern cover.



## BIBLIOGRAPHY

- Abe, M., Izaki, J., Miguchi, H., Masaki, T., Makita, A., and Nakashizuka, T. 2002. The effects of *Sasa* and canopy gap formation on tree regeneration in an old beech forest. *Journal of Vegetation Science*. 13: 565-574.
- Abrams, M.D. 1992. Fire and the development of oak forests. *Bioscience*. 42: 335 - 364.
- Allegheny National Forest. 1995. Management area 3. 0, 6000 plot survey report Appendix L in Analysis of timber harvest program capability 1995 through 2005. USDA Forest Service, Allegheny National Forest, Warren, Pennsylvania, USA.
- Allen, R.B., I. J. Payton, and J. E. Knowlton 1984. Effects of ungulates on structure and species composition in the Urewara forests as shown by exclosures. *N.Z. Journal of Ecology*. 7: 119-130.
- Alverson WS and DM Waller. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. pp. 280-297 in W. McShea and J. Rappole, eds., *The Science of Overabundance: Deer ecology and population management*, Smithsonian Inst. Press, Washington, DC.
- Anderson, J. P., Jr., & R.E. Egler. 1988. Patch studies in the stability of non-diversity: *Dennstaedtia*, *Solidago*, *Spiraea*, *Kalmia*. *Phytologia*. 64: 349 - 364.
- Antos, J.A., Parish, R., and Conley, K. 2000. Age structure and growth of the tree seedling bank in subalpine spruce-fir forests of south-central British Columbia. *American Midland Naturalist*. 143: 342-354.
- Arrington DA, Toth LA, Koebel JW (1999) Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. *Wetlands* 19:535-544
- Attiwill, P.M. and Adams, M.A. 1993. Tansley Review No. 50. Nutrient cycling in forests. *New Phytol*. 124: 561-582.
- Aubin, I., M. Beaudet, and C. Messier 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. *Canadian Journal of Forest Research*. 30: 168-177.

- Aubin, I., M. Beaudet, and C. Messier 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. *Canadian Journal of Forest Research* 30: 168-177.
- Augustine, D.J. and DeCalesta, D. 2003. Defining deer overabundance and threats to forest communities: from individual plants to landscape structure. *Ecoscience* 10: 472 - 486.
- Bailey, S.W., Horsley, S.B., and Long, R.P. 2005. Thirty years of change in forest soils of the Allegheny Plateau, Pennsylvania. *Soil Science Society of America Journal* 69: 681 - 690.
- Bailey, S.W., Horsley, S.B., Long, R.P., and Hallett, R.A. 2004. Influence of edaphic factors on sugar maple nutrition and health on the Allegheny Plateau. *Soil Science Society of America Journal* 68: 243 - 252.
- Baker, F.S. 1949. A revised tolerance table. *Journal of Forestry* 47: 179 - 181.
- Banta, J.A., Royo, A.A., Kirschbaum, C. and Carson, W.P. 2005. Boulders in the Allegheny National Forest: Evidence for boulders as refugia from deer and as a bioassay of overbrowsing. *Natural Areas Journal* 25: 10 - 18.
- Batzer, H.O. and Popp, M.P. 1985. Forest succession following a spruce budworm outbreak in Minnesota. *Forestry Chronicles*. 61: 807-814.
- Beattie, A.J., Culver, D.C. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia, USA Forest. *Ecology* 62:107-115
- Beckage, B. Clark, J.S. 2005. Does predation contribute to tree diversity? *Oecologia* 143: 458 - 469.
- Beckage, B., and Clark, J.S. 2003. Seedling survival and growth of three forest tree species: The role of spatial heterogeneity. *Ecology*. 84: 1849 - 1861.
- Beckage, B., Clark, J.S., Clinton, B.D., and Haines, B.L. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: The effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research*. 30: 1617-1631
- Bergquist, J., Örlander, G., and Nilsson, U. 1999. Deer browsing and slash removal affect field vegetation on south Swedish clearcuts. *Forest Ecology and Management*. 114: 171 - 182.
- Berkowitz, A.R., Canham, C.D., and Kelly, V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology*. 76: 1156 - 1168.
- Bierzzychudek, P. 1982. The Demography of Jack-in-the-Pulpit *Arisaema triphyllum* a Forest Perennial That Changes Sex. *Ecological Monographs* 52:335-352.

- Bigelow, S.W. and Canham, C.D. 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. *Journal of Ecology* 90: 188 – 200
- Biring, B.S., P.G. Comeau and P.L. Fielder. 2003. Long-term effects of vegetation control treatments for release of Engelmann spruce from a mixed-shrub community in southern British Columbia. *Annals of Forest Science*. 60:681-690.
- Bjorkbom, J.C. 1979. Seed production and advance regeneration in Allegheny hardwood forests. USDA Forest Service Research Paper NE - 435, Northeastern Experiment Research Station, Broomhall, PA, USA. 10 pp.
- Bonser, S.P. and Reader, R.J. 1998. Species and biomass dependence of an indirect effect of vegetation on seedling recruitment. *Ecoscience* 5(2): 207 - 212.
- Bowers, M.A., Sacchi, C.F. 1991. Fungal mediation of a plant-herbivore interaction in an early successional plant community. *Ecology* 72:1032-1037
- Brach, A.R., McNaughton, S.J., and Raynal, D.J. 1993. Photosynthetic adaptability of two fern species of a northern hardwood forest. *American Fern Journal*. 83: 47-53.
- Bradley, R.L., Titus, B.D., and Fyles, J.W. 1997. Nitrogen acquisition and competitive ability of *Kalmia angustifolia* L., paper birch (*Betula papyrifera* Marsh.) and black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings grown on different humus forms. *Plant Soil*. 195: 209 - 220.
- Bray, J.R. 1956. Gap phase replacement in a maple-basswood forest. *Ecology* 37: 598-600.
- Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682 – 687.
- Brokaw, N.V.L., Busing, R.T. 2000. Niche versus chance and tree diversity in forest gaps. *Trends in Ecology and Evolution* 15:183 – 188
- Brokaw, N. V. L. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. *Trop. Ecol.* 24: 194-200.
- Brooks, D.M., Bodmer, R.E., Matola, S. 1997. Tapirs - Status Survey and Conservation Action Plan. - IUCN/SSC Tapir Specialist Group.
- Brown, J.H., Whitman, T.G., Ernest, S.K.M., Ghering, C.A. 2001. Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science* 293: 643 – 650.
- Brown, J.H. and Heske, E.J. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.

- Bryant, J.P., Provenze, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., DuToit, J.T. 1991. Interactions between woody plant and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology, Evolution, and Systematics* 22: 431 – 446.
- Bucyanayandi, J., Bergeron, J. and Mernard, J. 1990. Preference of meadow voles (*Microtus pennsylvanicus*) for conifer seedlings: chemical components and nutritional quality of bark of damaged and undamaged trees. *Journal of Chemical Ecology* 16: 2569 - 2579.
- Bunnell, F.L. 1990. Reproduction of salal (*Gaultheria shallon* Pursh.) under forest canopy. *Canadian Journal of Forest Research*. 20: 91-100.
- Burger, J.C. and Louda, S.M. 1994. Indirect versus direct effects of grasses on growth of a cactus (*Opuntia fragilis*): insect herbivory versus competition. *Oecologia* 99: 79 - 87.
- Burns, R.M. and Honkala, B.H. 1990. Summary of tree characteristics. in *Silvics of North America, Volume 2, Hardwoods*. Agriculture Handbook 654. USDA Forest Service, pp. 640 - 644.
- Cabin, R.J., Weller, S., Lorence, D., Flynn, T., Sakai, A., Sandquist, D., Hadway, L. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conservation Biology* 14:439-453.
- Campbell, T.E. 1981. Effects of endrin in repellent seed coverings on caged rodents. USDA Forest Service, SRS. Research Paper SO-174.
- Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548-550.
- Canham, C.D., Finzi, A.C., Pacala S. W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research*. 24: 37 - 349.
- Carson, W.P., Root, R.B. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia* 121:260-272.
- Carson, W.P., Root, R.B. 2000. Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70: 73-99.
- Carson, W. P., Cronin, J. P., Long, Z. T. 2004. A general rule for predicting when insects will have strong top-down effects on plant communities: on the relationship between insect outbreaks and host concentration. Pages in press In Weisser, W.W. and E. Siemann (eds). *Insects and Ecosystem Function*. Ecological Studies Series. Springer-Verlag.
- Casper, B.B. and Jackson, R.B. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545-570.

- Cater, T.C. and Chapin III, F.S. 2000. Differential effects of competition or microenvironment on boreal tree seedling establishment after fire. *Ecology* 81: 1086-1099
- Chaneton, E.J. and Bonsall, M.B. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos* 88: 380 - 394.
- Chang, S.X. and Preston, C.M. 2000. Understory competition affects tree growth and fate of fertilizer-applied 15N in a Coastal British Columbia plantation forest: 6-year results. *Canadian Journal of Forest Research*. 30: 1379-1388.
- Chang, S.X., Preston, C.M., McCullough, K., Weetman, G.F., and Barker, J. 1996a. Understory competition effect on distribution and recovery of 15N on a western red cedar - western hemlock cutover site on northern Vancouver Island. *Canadian Journal of Forest Research*. 26: 313-321.
- Chang, S.X., Weetman, G.F., and Preston, C.M. 1996b. Understory competition effect on tree growth and biomass allocation on a coastal old-growth forest cutover site in British Columbia. *Forest Ecology and Management*. 83: 1-11
- Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M., Case, T.J. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5: 302 – 315.
- Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. *Canadian Journal of Forest Research* 27:1383-1393
- Christy, E.J. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). *Vegetatio* 65: 21-28
- Cintra, R. 1997. A test of the Janzen-Connell model with two common tree species in Amazonian forest. *Journal of Tropical Ecology* 13(5): 641 – 658
- Clark D. B and Clark, D.A. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology*. 79: 447-457
- Clark, D.B., Clark, D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55: 225-230.
- Clark, D.L. and Wilson, M.V. 2003. Post-dispersal seed fates of four prairie species. *American Journal of Botany* 90: 730 - 735.
- Cline, A.C., Spurr, S.H. 1942. The virgin upland forest of central New England: A study of old growth stands in the Pisgah mountain section of southwestern New Hampshire. *Harv For Bul No.* 21 58 pp.



- Clinton, B.D. and Vose, J.M. 1996. Effects of *Rhododendron maximum* L. on *Acer rubrum* L. seedling establishment. *Castanea* 6: 38-45.
- Clinton, B.D., Boring, L.R., and Swank, W.T. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the Southern Appalachians: Influences of topographic position and evergreen understory. *American Midland Naturalist*. 132: 308 - 319.
- Cody, W.J., Hall, I.V., and Crompton, C.W. 1977. The biology of Canadian weeds Part 26: *Dennstaedtia punctilobula*. *Canadian Journal of Plant Science*. 57: 1159-1168
- Coley, P.D., Bryant, J.P., Chapin III, F.S. 1985. Resource availability and plant antiherbivore defense. *Science* 230: 895 – 899.
- Collins, B.S., Pickett, S.T.A. 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *Journal of Ecology* 76:437 – 450.
- Collins, R.J. and Carson, W.P. 2003. The fire and oak hypothesis: incorporating the effects of deer browsing and canopy gaps. In *Proceedings of the 13th Central Hardwood Forest Conference*. Urbana-Champaign IL. April 1-3 2002. USDA Forest Service North Central Research Station General Technical Report NC-234.
- Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. In: den Boer PJ, Gradwell GR (eds) *Dynamics of Populations*. Oosterbeek, the Netherlands, pp 298 – 310.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302 – 1310.
- Connell, J.H. 1983. Prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122: 661–696.
- Connell, J.H. 1989. Some processes affecting the species composition in forest gaps. *Ecology* 70: 560-562.
- Connell, J.H. 1990. Apparent vs real competition in plants. In J.B. Grace and D. Tilman (eds.) *Perspectives on plant competition*. Academic Press, San Diego, CA. pp. 9-25.
- Connell, J.H., Tracey, J.G., Webb, L.J. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs* 54:141-164.
- Connell, J.H. and Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. *Am. Nat.* 121: 789-824.

- Connell, J.H., Lowman, M.D., and Noble, I.R. 1997. Subcanopy gaps in temperate and tropical forests. *Australian Journal of Ecology* 22: 163-168
- Coomes, D.A. and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs*. 70: 171-207.
- Coomes, D.A., Allen, R.B., Forsyth, D.M., and Lee, W.G. 2003. Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conserv. Biol.* 17: 450-459.
- Côte, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., and Waller, D.M. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* 35: 113 - 147.
- Crawley, M. J. 1990. The population dynamics of plants. *Philosophical Transactions of the Royal Society of London* 330: 125-140.
- Croat, T.B. 1978. *Flora of Barro Colorado Island*. Stanford University Press. Stanford, California.
- Cunningham, A. 1979. A century of change in the forests of the Ruahine Range, North Island, New Zealand: 1870 - 1970. *New Zealand Journal of Ecology*. 2: 11-21.
- Dall, S.R.X., Kotler, B.P., and Bouskila, A. 2001. Attention, 'apprehension' and gerbils searching in patches. *Annals of Zoology Fennici* 38: 15 - 23.
- Davies, R. J. 1985. The importance of weed control and the use of tree shelters for establishing broadleaved trees on grass-dominated sites in England. *Forestry* 58: 167-180.
- de la Cretaz, A.L. and Kelty, M.J. 1999. Establishment and control of hay-scented fern: a native invasive species. *Biological Invasions* 1: 223-236
- de la Cretaz, A.L. and Kelty, M.J. 2002. Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. *Restoration Ecology*. 10: 416-426
- deCalesta, D. S., and S. L. Stout. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildlife Society Bulletin* 25:252-258.
- Den Ouden, J. 2000. The role of bracken (*Pteridium aquilinum*) in forest dynamics, Ph.D. thesis. Wageningen University, The Netherlands; 218 pp.
- Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431-452.
- Denslow, S.J., Newell, E., and Ellison, A.M. 1991. The effect of understory palms and cyclanth on the growth and survival of *Inga* seedlings. *Biotropica*. 23: 225-234.

- De Steven, D. 1991, Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth: *Ecology*. 72: 1076-1088.
- De Steven, D., Putz, F.E. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipterix panamensis*. *Oikos* 43: 207 – 216.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H., and Forseth, I.N. 1993. Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *American Journal of Botany* 80: 244-252
- Dirzo, R., Horvitz, C., Quevedo, H., Lopez, M.A. 1992. The effects of gap size and age on the understory herb community of a tropical Mexican rain forest. *Journal of Ecology* 80: 809-822.
- Dirzo, R., Miranda, A. 1990. Contemporary neotropical defaunation and forest structure, function, and diversity-a sequel to John Terborgh. *Conservation Biology* 4: 444-447.
- Dirzo, R., Miranda, A. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. In: Price PW, Lweinsohn TM, Fernandes GW, Benson WW (eds) *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*. Wiley and Sons, New York, pp. 273-287.
- Doak, D.F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* 73: 2086 – 2099.
- Dolling, A. 1996. Interference of bracken (*Pteridium aquilinum* L. Kuhn) with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) seedling establishment. *Forest Ecology and Management*. 88: 227-235.
- Dolling, A. 1999. The vegetative spread of *Pteridium aquilinum* in a hemiboreal forest: Invasion or revegetation? *Forest Ecology and Management*. 124: 177-184.
- Dolling, A., Zackrisson, O., and Nilsson, M.C. 1994. Seasonal variation in the phytotoxicity of bracken (*Pteridium aquilinum* L. Kuhn). *Journal of Chemical Ecology* 20: 3163-3172.
- Donlan, C.J., Tershy, B.R., Croll, D.A. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. *Journal of Applied Ecology* 39: 235 – 246.
- Donlan, B.J. and Parker, G.R. 2004. Understory response to disturbance: an investigation of prescribed burning and understory removal treatments. In *Proceedings: Upland oak ecology symposium: history, current conditions, and sustainability*. General Technical Report SRS-73.

- Drew, A.P. 1988. Interference of black cherry by ground flora of the Allegheny uplands. *Canadian Journal of Forest Research* 24: 652 - 656.
- Edwards GR, Crawley MJ (1999) Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 118: 288-296
- Edwards, G.R. and Crawley, M.J. 1999. Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 118: 288 - 296.
- Ehrenfeld, J.G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. *Bull. Torrey Bot. Club.* 107: 29-41.
- Ehrlen, J. 1995. Demography of the perennial herb *Lathyrus vernus* II. Herbivory and population dynamics. *Journal of Ecology* 83: 297 – 308.
- Emmons, L.H., Feer, F. 1997. Neotropical rainforest mammals: A field guide. Second Edition. University of Chicago Press, Chicago.
- English, B. and Hackett, R. 1994. The impact of *Kalmia* on plantation performance in central Newfoundland. *Silvicultural Notebook Series Vol. 2.*
- Erdmann, G.G., Metzger, F.T., and Obert, R.R. 1979. Macronutrient deficiency symptoms in seedlings of four northern hardwoods. USDA Forest Service General Technical Report NC-53. 36 pp.
- Facelli, J.M. and Pickett, S.T.A. 1991. Plant litter: Its dynamics and effects on plant community structure. *Botanical Reviews* 57 : 1-32.
- Farris-Lopez, K., Denslow, J.S., Moser, B., and Passmore, H. 2004. Influence of a common palm, *Oenocarpus mapora*, on seedling establishment in a tropical moist forest in Panama. *Journal of Tropical Ecology* 20: 429 - 438.
- Feeny, P. 1976. Plant apparency and chemical defence. In: Wallace JW, Nansel RL (eds) *Biological Interactions between plants and insects. Recent Advances in Phytochemistry* (10). Plenum Press, New York.
- Ferguson, D.E. and Adams, D.L. 1994. Effects of pocket gophers, bracken fern, and western coneflower on survival and growth of planted conifers. *Northwest Science* 68: 241 - 249.
- Finzi, A.C., and Canham, C.D. 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. *Forest Ecology and Management* 131: 153 - 165.
- Foster, R.B., Brokaw, N.V.L. 1996. Structure and history of the vegetation of Barro Colorado Island. In: Leigh EG, Rand AA, Windsor DM (eds) *The ecology of a tropical forest: seasonal rhythms and long-term changes.* Smithsonian Institution Press, Washington DC

- Foster, D.R., Motzkin, G., and Slater, B. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* 1: 96 - 119.
- Frak, E. and Ponge, J.F. 2002. The influence of altitude on the distribution of subterranean organs and humus components in *Vaccinium myrtillus* carpets. *Journal of Vegetation Science*. 13: 17 - 26.
- Franklin, J.F. and Pechanec, A.A. 1967. Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities. In *Biology of alder: Proceedings of a Symposium Held at Northwest Scientific Association 40th Annual Meeting, 14 - 15 April 1967*, Pullman, WA. Edited by J. Trappe, J. Franklin, R.F. Tarrant, and G.M. Hansen. pp. 37 - 43.
- Fuerst, E.P. and Putnam, A.R. 1983. Separating the competitive and allelopathic components of interference: Theoretical principles. *Journal of Chemical Ecology* 20: 1355-1380.
- Fujisaka, S., Escobar, G., Veneklaas, E. 1998. Plant community diversity relative to human land uses in an Amazon forest colony. *Biodiversity Conservation* 7: 41 – 57.
- Fuller, J.L., Foster, D.R., McLachlan, J.S., and Drake, N. 1998. Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems* 1: 76 - 95.
- Galeano, G., Suarez, S., Balslev, H. 1998. Vascular plant species count in a wet forest in the Choco area on the Pacific coast of Colombia. *Biodiversity Conservation* 7: 1563-1575.
- Gentry, A.H. 1990. *Four Neotropical Forests*. Yale University Press, New Haven, CT
- Gentry, A.H., Dodson, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19: 149-156.
- George, L.O. and Bazzaz, F.A. 1999a. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. *Ecology* 80: 833-845
- George, L.O. and Bazzaz, F.A. 1999b. The fern understory as an ecological filter: Growth and survival of canopy-tree seedlings. *Ecology* 80: 846-856.
- Gerwing, J.J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *Journal of Applied Ecology* 38: 1264-1276.
- Ghent, A.W., Fraser, D.A., and Thomas, J.B. 1957. Evidence of trends in forest succession during the first decade following budworm devastation. *Forest Science* 2: 184-208.
- Gill, D.S. and Marks, P.L. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61: 183-205

- Gillman, L.N., Ogden, J. 2003. Seedling mortality and damage due to non-trophic animal interactions in a northern New Zealand forest. *Australian Ecology* 28: 48-52.
- Gillman, L.N., Wright, S.D., and Ogden, J. 2003. Response of forest tree seedlings to simulated litterfall damage. *Plant Ecology* 169: 53-60.
- Givnish, T.J. 2002. On the adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* 36: 703-743.
- Gliessman, S.R. 1978. The establishment of bracken following fire in tropical habitats. *American Fern Journal*. 68: 41-44.
- Gliessman, S.R. and Muller, C.H. 1972. The phytotoxic potential of bracken, *Pteridium aquilinum* (L.) Kuhn. *Madrono* 21: 299-304.
- Gliessman, S.R. and Muller, C.H. 1978. The allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. *Journal of Chemical Ecology* 4: 337-362.
- Godley, E.J. and Smith, D.H. 1981. Breeding systems in New Zealand *Pseudowintera colorata* (Winteraceae). *N.Z. J. Bot.* 19: 151 - 156.
- Godman, R.M., Yawney, H.W., and Tubbs, C.H. 1990. *Acer saccharum* Marsh. Sugar Maple. in *Silvics of North America, Volume 2, Hardwoods*. USDA Forest Service Agricultural Handbook.
- Gonzalez, M.E., Veblen, T.T., Donoso, C., and Valeria, L. 2002. Tree regeneration responses in a lowland Nothofagus-dominated forest after bamboo dieback in south-central Chile. *Plant Ecol.* 161: 59-73.
- Gordon, I.J., Hester, A.J., Festa-Bianchet, M. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41: 1021 - 1031.
- Gratzer, G., Raj, P.B., and Glatzel, G. 1999. The influence of the bamboo *Yushania microphylla* on the regeneration of *Abies densa* in central Bhutan. *Canadian Journal of Forest Research*. 29: 1518 - 1527.
- Grauel, W.T. and Putz, F.E. 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *Forest Ecology and Management*. 190: 99-108.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D.D., Morin, H., Charron, L., and Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*. 29: 824-839.

- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169 – 1194.
- Griscom, B.W. and Ashton, P.M.S. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. *Forest Ecology and Management*. 175: 445 - 454.
- Guariguata, M.R. 1990. Landslide disturbance and forest regeneration in the Upper Luquillo mountains of Puerto Rico. *Journal of Ecology*. 78: 814-832.
- Guariguata, M.R. 1998. Response of forest tree saplings to experimental damage in lowland Panama. *Forest Ecology and Management*. 102: 103-111.
- Gurevitch, J.J., Morrison, A. & Hedges, L.V. 2000. The interaction between competition and predation: a meta-analysis of field experiments. *American Naturalist* 155: 435–453.
- Gutierrez, J.R., Meserve, P.L., Herrera, S., Contreras, L.C., Jaksic, F.M. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia* 109: 398-406.
- Hall, I.V., Jackson, L.P., and Everett, C.F. 1973. The biology of Canadian weeds. 1. *Kalmia angustifolia* L. *Canadian Journal of Plant Science* 53: 865-873.
- Hambäck, P.A., Beckerman, A.P. 2003. Herbivory and plant resource competition: a review of two interacting interactions. *Oikos* 101: 26 – 37.
- Hammond, D.S., Brown, V.K. 1998. Disturbance, phenology, and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In: Newberry DM, Prins HHT, Brown ND (eds) *Dynamics of Tropical Communities*. Blackwell, Oxford, pp. 51 – 78.
- Hannah, P.R. 1988. The shelterwood method in northeastern forest types: a literature review. *Northern Journal of Applied Forestry* 5: 70 - 77.
- Hannah, P.R. 1993. Composition and development of two Appalachian hardwood stands in North Carolina. *The Journal of the Elisha Mitchell Scientific Society* 109: 87 - 98.
- Harper, J.L. 1977. *The Population Biology of Plants*. Academic Press, London.
- Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. In *Tropical Trees as Living Systems*. Cambridge University Press, London. pp. 617-638.
- Haukioja, E., Koricheva, J. 2000. Tolerance to herbivory in woody vs. herbaceous plants. *Evolutionary Ecology* 14: 551-562.
- Haywood, J.D., Goelz, J.C., Sword-Sayer, M.A., Tiarks, A.E. 2003. Influence of fertilization, weed control, and pine litter on loblolly pine growth and productivity and understory plant

- development through twelve growing seasons. *Canadian Journal of Forest Research*. 33: 1974 - 1982.
- Healy, W. M. 1971. Forage preferences of tame deer in a northwest Pennsylvania clear-cutting. *Journal of Wildlife Management* 35:717-723.
- Hewitt, N. 1998. Seed size and shade tolerance: A comparative analysis of North American temperate trees. *Oecologia* 114: 432 - 440.
- Hill, J.D. 1996. Population dynamics of hay-scented fern (*Dennstaedtia punctilobula*) and its impact on forest composition, structure, and dynamics. Storrs, CT, University of Connecticut.
- Hill, J.D. Population dynamics of hayscented fern (*Dennstaedtia punctilobula*) and its impact on forest composition, structure, and dynamics. 1996. Storrs, CT, University of Connecticut
- Hill, J.D., and J. A. Silander, Jr. 2001. Distribution and dynamics of two ferns: *Dennstaedtia punctilobula* (Dennstaedtiaceae) and *Thelypteris noveboracensis* (Thelypteridaceae) in a Northeast mixed hardwoods-hemlock forest. *American Journal of Botany* 88: 894-902.
- Hille Ris Lambers, J. and Clark, J.S. 2003. Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Canadian Journal of Forest Research*. 33: 783 - 795.
- Hix, D.M., Fosbroke, D.E., Hicks Jr., R.R., and Gottschalk, K.W. 1991. Development of regeneration following gypsy moth defoliation of Appalachian Plateau and Ridge and Valley hardwood stands. In *Proceedings, 8th Central Hardwood Forest Conference*. USDA Forest Service General Technical Report NE-148., Radnor, PA. pp. 347-359.
- Hogg, E.H. and Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. *Canadian Journal of Forest Research*. 21: 387-394.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197-229.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 142: 623-645
- Horsley, S.B. 1977. Allelopathic inhibition of black cherry. II. Inhibition by woodland grass, ferns, and club moss. *Canadian Journal of Forest Research*. 7: 515-519.
- Horsley, S.B. 1981. Control of herbaceous weeds in Allegheny hardwood forests with herbicides. *Weed Science* 29: 655 - 662.



- Horsley, S.B. 1982. Development of reproduction in Allegheny hardwood stands after herbicide-clearcuts and herbicide-shelterwood cuts. USDA Forest Service Research Note NE-308, Northeastern Experimental Station, Broomhall, PA. 4 p.
- Horsley, S.B. 1985. Reforestation of orchard stands and savannahs on Pennsylvania's Allegheny Plateau. *Northern Journal of Applied Forestry* 2: 22-26.
- Horsley, S.B. 1993a. Mechanisms of interference between hay-scented fern and black cherry. *Canadian Journal of Forest Research*. 23: 2059-2069.
- Horsley, S.B. 1993b. Role of allelopathy in hay-scented fern interference with black cherry regeneration. *Journal of Chemical Ecology* 19: 2737-2755.
- Horsley, S.B. and Marquis, D.A. 1983. Interference by weeds and deer with Allegheny Pennsylvania USA hardwood reproduction. *Canadian Journal of Forest Research*. 13: 61-69.
- Horsley, S.B., Stout, S.L., and DeCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13: 98 - 113.
- Horvitz, C. 1991. Light environments, stage structure, and dispersal syndromes of Costa Rican Marantaceae. In Huxley CR, Cutler DF (eds) *Ant-Plant Interactions*. Oxford University Press, Oxford, UK, pp. 463-485.
- Hough, A.F. 1936. Height growth of hemlock and hardwood seedlings in a virgin stand on East Tionesta Creek. USDA Forest Service Technical Note # 12, Allegheny Forest Experiment Station, Philadelphia, PA, USA.
- Hough, A.F. 1949. Deer and rabbit browsing and available winter forage in Allegheny hardwood forests. *Journal of Wildlife Management* 13: 135 – 141.
- Hough, A.F. 1965. A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. *Ecology* 46: 370 - 373.
- Houle, G. 1990. Regenerative traits of tree species in a deciduous forest of northeastern North America. *Holarctic Ecology* 14: 142 - 151.
- Howe, H.F., Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201 – 223.
- Howe, H.F. and Brown, J.S. 2001. The ghost of granivory past. *Ecology Letters* 4: 371-378
- Huenneke, L.F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bulletin of the Torrey Botanical Club* 110: 170-175.

- Hulme P.E. 1996. Herbivory, plant regeneration and species coexistence. *Journal of Ecology* 84: 609 - 615
- Hulme, P.E. 1994. Seedling herbivory in a grassland: Relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* 82: 873-880
- Hulme, P.E. and Borelli, T. 1999. Variability in post-dispersal seed predation in deciduous woodland: Relative importance of location, seed species, burial and density. *Plant Ecology* 145: 149 - 156.
- Hulme, P.E. and Hunt, M.K. 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology*. 68: 417 - 428.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 22:477 – 503.
- Husheer, S.W., Coomes, D.A., and Robertson, A.W. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *Forest Ecology and Management*. 181: 99 - 117.
- Ickes, K., Dewalt, S.J., Appanah, S. 2001. Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology* 17: 191-206.
- Iida, S. 2004. Indirect negative influence of dwarf bamboo on survival of *Quercus* acorn by hoarding behavior of wood mice. *Forest Ecology and Management*. 202: 257 - 263.
- Inderjit and Callaway, R.M. 2003. Experimental designs for the study of allelopathy. *Plant and Soil* 256: 1-11.
- Inderjit and Mallik, A.U. 1996. The nature of interference potential of *Kalmia angustifolia*. *Canadian Journal of Forest Research*. 26: 1899-1904
- Inouye, R., Huntly, N., Tilman, D., Tester, J.R. 1987. Pocket gophers, (*Geomys bursarius*), vegetation and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* 72:178-184.
- Ivan, J.S. and Swihart, R.K. 2000. Selection of mast by granivorous rodents of the central hardwood forest region. *Journal of Mammalogy* 81: 549-562.
- Jacobs, Rodney D. 1969. Growth and development of deer browsed sugar maple seedlings. *Journal of Forestry* 67(12):870-874.

- Jäderlund, A., Zackrisson, O., Dahlberg, A., and Nilsson, M.C. 1997. Interference of *Vaccinium myrtillus* on establishment, growth, and nutrition of *Picea abies* seedlings in a northern boreal site. *Canadian Journal of Forest Research* 27: 2017-2025.
- Jandl, R., Starlinger, F., Englisch, M., Herzberger, E., and Johann, E. 2005. Long-term effects of a forest amelioration experiment. *Canadian Journal of Forest Research* 32: 120 - 128.
- Jane, G.T. and Pracy, L.T. 1974. Observations on two animal exclosures in Haurangi Forest over a period of 20 years (1951 - 1971). *New Zealand Journal of Forestry* 19: 102-113.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104: 501-528.
- Jones, R.H., Sharitz, R.R., Dixon, P.M., Segal, D.S., Schneider, R.L. 1994. Woody plant regeneration in four floodplain forests. *Ecological Monographs* 64: 345 – 367.
- Kappelle, M., Van Omme, L., Juarez, M.E. 2000. Lista de la flora vascular de la cuenca superior del Rio Savegre, San Gerardo de Dota, Costa Rica. *Acta Botanica Mexicana* 51: 1-38.
- Kelly, V.R. and Canham, C.D. 1992. Resource heterogeneity in oldfields. *Journal of Vegetation Science* 3: 545-552.
- Killeen, T.J., Jardim, A., Mamani, F., Rojas, N. 1998. Diversity, composition and structure of a tropical semideciduous forest in the Chiquitanía region of Santa Cruz, Bolivia. *Journal of Tropical Ecology* 14: 808 – 827.
- Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. *Soil Science Society of American Journal* 60: 1643-1654.
- Knight, T.M. 2003. Effects of herbivory and its timing across populations of *Trillium grandiflorum* (Liliaceae). *American Journal of Botany* 90(8): 1207 – 1214.
- Kobe, R.S., Pacala, S.W., Silander, J.A., Jr., Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications* 5: 517 - 532
- Kochummen, K.M. and Ng, F.S.P. 1977. Natural plant succession after farming in Kepong. *The Malaysian Forester* 40: 61-78.
- Kolb, T.E., T.W. Bowersox, and L.H. McCormick. 1990. Influences of light intensity on weed-induced stresses of tree seedlings. *Canadian Journal of Forest Research* 20: 503-507.
- Kollman, J. and Buschor, M. 2002. Edge effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* 164: 249 - 261.

- Kollman, J., Coomes, D.A., and White, S.M. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years, and sites. *Functional Ecology* 12: 683 - 690.
- Koop, H. and Hilgen, P. 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *Forest Ecology and Management*. 20: 135 - 150.
- Kotanen, P.M. 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs on a Californian Coastal Prairie. *Ecography* 18: 190 -199.
- Kotler, B.P., Brown, J.S. and Bouskila, A. 2004. Apprehension and time allocation in gerbils: The effects of predatory risk and energetic state. *Ecology* 85: 917 - 922.
- Kotler, B.P., Brown, J.S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72: 2249 - 2260.
- Kransy, M.E. and DiGregorio, L.M. 2001. Gap dynamics in Allegheny northern hardwood forests in the presence of beech bark disease and gypsy moth disturbances. *Forest Ecology and Management* 144: 265 - 274.
- Kransy, M.E. and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in the Allegheny northern hardwood forests. *Canadian Journal of Forest Research* 22: 139 - 143.
- Krause, H.H., Weetman, G.F., and Arp, P.A. 1978. Nutrient cycling in boreal forest ecosystems of North America. In *Proceedings of the 5th North American Forest Soils Conference*. Colorado State University, Ft. Collins, CO.
- Kurmis, V., and Sucoff, E. 1989. Population density and height distribution of *Corylus cornuta* in undisturbed forests of Minnesota: 1965-1984. *Canadian Journal of Botany* 67:2409-2413.
- Latham, R. E., J. Beyea, M. Benner, C. A. Dunn, M. A. Fajvan, R. Freed, S. B. Horsley A. F., Rhoads and B. P. Shissler. 2005. Managing White-tailed Deer in Forest Habitat from an Ecosystem Perspective: Pennsylvania Case Study. Audubon Pennsylvania and the Pennsylvania Habitat Alliance, Harrisburg. 340 pp.
- Latham, R.E. 2003. Shrubland longevity and rare plant species in the northeastern United States. *Forest Ecology and Management*. 185: 21-39.
- Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44: 427 – 433.

- Lei, T.T., Semones, S.W., Walker, J.F., Clinton, B.D., and Nilsen, E.T. 2002. Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. *International Journal of Plant Science* 163: 991-1000.
- Leigh, E.G., Rand, A.A., Windsor, D.M. (eds) 1996. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington DC
- Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., and Lavelle, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London, Section B*. 270: 775-781.
- Lidicker, W.Z., Wolff, J.O., Lidicker, L.N., and Smith, M.H. 1992. Utilization of a habitat mosaic by cotton rats during a population decline. *Landscape Ecology* 6: 259-268
- Lieffers, V.J., Macdonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. *Canadian Journal of Forest Research*. 23: 2070-2077.
- Lipscomb, M.V. and Nilsen, E.T. 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast and southwest slopes of the southern Appalachian mountains. I. Irradiance tolerance. *American Journal of Botany* 77: 108-115.
- Löf, M. 2000. Establishment and growth in seedlings of *Fagus sylvatica* and *Quercus robur*: influence of interference from herbaceous vegetation. *Canadian Journal of Forest Research*. 30: 855 - 864.
- Long, R.P., Horsley, S.B., Lilja, P.R. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. *Canadian Journal of Forest Research* 27:1560 - 1573.
- Longland, W.S. and Price, M.V. 1991. Direct observations of owls and heteromyid rodents: Can predation risk explain microhabitat use? *Ecology* 72: 2261 - 2273.
- Lu, K., Mesler, M. 1981. Ant dispersal of a Neotropical forest floor gesneriad. *Biotropica* 13:159-160.
- Lusk, C.H. 2001. When is a gap not a gap? Light levels and leaf area index in bamboo-filled gaps in a Chilean rain forest. *Gayana Botanica*. 58: 25-30
- Lutz, H.J. 1930. The vegetation of Heart's Content, a virgin forest in northwestern Pennsylvania. *Ecology* 11: 1 - 29.
- Lyon, J. and Sharpe, W.E. 1996. Hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) interference with growth of northern red oak (*Quercus rubra* L.) seedlings. *Tree Physiology* 16: 923 - 932.

- Magurran, A.E. 198. Ecological diversity and its measurement. Princeton University Press, NJ.
- Maheswaran, J. and Guatilleke, I.A.U.N. 1988. Litter decomposition in a lowland rain forest and a deforested area in Sri Lanka. *Biotropica*. 20: 90 - 99.
- Mallik, A.U. 1995. Conversion of temperate forests into heaths: Role of ecosystem disturbance and ericaceous plants. *Environmental Management* 19: 675-684.
- Mallik, A.U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: Role of disturbance, seedbed limitation, and keystone species change. *Critical Reviews in Plant Science* 22: 341-366.
- Mallik, A.U. and Inderjit. 2001. *Kalmia angustifolia*: ecology and management. *Weed Technology* 15: 858 – 866.
- Mancinelli, A.L. 1994. The physiology of phytochrome action. In *Photomorphogenesis in Plants*, 2nd edn. Eds. R. E. Kendrick and G. H. M. Kronenberg. Kluwer Academic Press, Dordrecht. pp. 211-269
- Manson, R.H. and Stiles, E.W. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82: 37-50.
- Manson, R.H., Ostfeld, R.S. and Canham, C.D. 2001. Long-term effects of rodent herbivores on tree invasion dynamics along forest-field edges. *Ecology* 82: 3320 - 3329.
- Marks, P.L. and Gardescu, S. 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. *Journal of the Torrey Botanical Society* 125: 287-296
- Marquis, D.A. 1973. The effect of environmental factors on advance regeneration of Allegheny hardwoods. Yale University, New Haven, CT, USA.
- Marquis, D.A. 1974. The impact of deer browsing in Allegheny hardwood regeneration. USDA Forest Service Research Paper NE-308. Northeastern Forest Experiment Station, Upper Darby, PA.
- Marquis, D.A. 1975. Seed storage and germination under northern hardwood forests. *Canadian Journal of Forest Research* 5: 478 - 484.
- Marquis, D.A. 1979. Shelterwood cutting in Allegheny hardwoods. *Journal of Forestry* 77: 40 - 144.
- Marquis, D.A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests on northwestern Pennsylvania. USDA Forest Service Research Paper NE - 475. Northeastern Forest Experiment Station, Broomall, PA, USA.

- Marquis, D.A. 1989. Forests of the Northeast: History and future trends. In Proceedings of the Penn State Forest Resources Issues Conference: Timber management and its effect on wildlife, Finley, J.C. and Brittingham, M.C., eds. April 4 - 6, 1989, University Park, PA, USA. Pgs. 14 - 25.
- Marquis, D.A. 1990. *Prunus serotina* Ehrh. Black Cherry. in Silvics of North America, Volume 2, Hardwoods. USDA Forest Service Agricultural Handbook. pgs. 594 - 604.
- Marquis, D.A., Ernst, R.L., Stout, S.L. 1992. Prescribing silvicultural treatments in hardwood stands of the Alleghenies (revised). USDA Forest Service, GTR-NE-96. Radnor, PA.
- Marrs, R.H., Johnson, S.W., Le Duc, M.G. 1998. Control of bracken and restoration of heathland. VIII. The regeneration of the heathland community after 18 years of continued bracken control or 6 years of control followed by recovery. Journal of Applied Ecology 35: 857 - 870.
- Maubon, M., Ponge, J.F., and Andre, J. 1995. Dynamics of *Vaccinium myrtillus* patches in mountain spruce forest. Journal of Vegetation Science. 6: 343-348.
- May, T. 2000. Respuesta de la vegetacion en un calimetal de *Dicranopteris pectinata* despues de un fuego, en la parte oriental de la Cordillera Central, Republica Dominicana. Moscosoa 11: 113-132.
- Mayfield, M.M., Daily, G.C. 2004. Countryside biogeography of Neotropical herbaceous and shrubby plants. Ecological Applications In press.
- McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environmental Review 9: 1-59.
- McCracken, K.E., Witham, J.W., and Hunter, J.L., Jr. 1999. Relationships between seed fall of three tree species and *Peromyscus leucopus* and *Clethrionomys gapperi* during 10 years in an oak-pine forest. Journal of Mammalogy 80: 1288 - 1296.
- McLachlan, S.M., Bazely, D.R. 2001. Recovery patterns of understory herbs and their use as indicators of deciduous forest regeneration. Conservation Biology 15: 98-110.
- McPhee, C. and Aarssen, L. 2001. The separation of above-and belowground competition in plants: A review and critique of methodology. Plant Ecology 152: 119-136.
- McShea, W.J., Underwood, H.B., and Rappole, J.H. 1997. The science of overabundance: Deer ecology and population management. Smithsonian Institution Press, Washington DC.
- McWilliams, William H.; Stout, Susan L.; Bowersox, Todd W.; McCormick, Larry H. 1995. Adequacy of advance tree-seedling regeneration in Pennsylvania's forests. Northern Journal of Applied Forestry 12:187-191.

- Meades, W.J. 1983. Heathlands. In Biogeography and ecology of the island of Newfoundland. G.R. South, ed. Dr. W. Junk, The Hague, The Netherlands. pp. 267 - 318.
- Messier, C. 1992. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of *Gaultheria shallon*. Canadian Journal of Botany 70: 2271-2276.
- Messier, C. 1993. Factors limiting early growth of western red cedar, western hemlock and Sitka spruce seedlings on ericaceous-dominated clearcut sites in coastal British Columbia. Forest Ecology and Management. 60: 181-206.
- Messier, C. and Kimmins, J.P. 1991. Above- and belowground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia. Forest Ecology and Management. 46: 275 - 294.
- Messier, C. and Kimmins, J.P. 1990. Nutritional stress in *Picea sitchensis* plantation in coastal British Columbia: the effects of *Gaultheria shallon* and declining site fertility. Water, Air, Soil Pollution 54: 257-267.
- Messier, C., Honer, T.W., and Kimmins, J.P. 1989. Photosynthetic photon flux density, red to far-red ratio, and minimum light requirement for survival of *Gaultheria shallon* in western red cedar-western hemlock stands in coastal British Columbia (Canada). Canadian Journal of Forest Research 19: 1470-1477.
- Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science. 9: 511-520.
- Michelsen, A., Schmidt, I.K., Jonasson, S., Dighton, J., Hones, H.E., and Callaghan, T.V. 1995. Inhibition of growth and effects on nutrient uptake of arctic graminoids by leaf extracts - allelopathy or resource competition between plants and microbes? Oecologia 103: 407-418.
- Milton, W.E.J. 1940. The effect of manuring, grazing and liming on the yield, botanical and chemical composition of natural hill pastures. Journal of Ecology 28: 326 - 356
- Mladenoff, D.J. And Stearns, F. 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes Region: a re-examination and model simulation. Conservation Biology 7: 889 - 900.
- Moles, A.T., Warton, D.I., and Westoby, M. 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? Ecology 84: 3148 - 3161.
- Monk, C.D., McGinty, D.T., and Day Jr., F.P. 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. Bulletin of the Torrey Botanical Society 112: 187-193.



- Montgomery, R.A. 2004. Effects of understory foliage on patterns of light attenuation near the forest floor. *Biotropica* 36: 33 – 39.
- Moola, F.M. and Mallik, A.U. 1998. Morphological plasticity and regeneration strategies of velvet leaf blueberry (*Vaccinium myrtilloides* Michx.) following canopy disturbance in boreal mixed wood forests. *Forest Ecology and Management*. 111: 35-50.
- Moore, M.R. and Vankat, J.L. 1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. *American Midland Naturalist* 115:336-347.
- Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24: 730 – 741.
- Morin, R. S., Liebhold, A. M., Gottschalk, K. W., Twardus, D. B., Acciavatti, R.E., White, R.L., Horsley, S. B., Smith, W. D., Luzador, E. R. 2001. Forest health conditions on the Allegheny National Forest (1989-1999): analysis of forest health monitoring surveys. NA-TP-04-01. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Area, State and Private Forestry. 68 p.
- Muller, C. 1969. Allelopathy as a factor in ecological process. *Vegetatio* 18: 348-357.
- Muzika, R.M. and Twery, M.J. 1995. Regeneration in defoliated and thinned hardwood stands of north-central West Virginia. In *Proceedings, 10th Central Hardwood Forest Conference*. USDA Forest Service General Technical Report NE-197, Radnor, PA. pp. 326-340.
- Nakashizuka, T. 1987. Regeneration dynamics of beech forests in Japan. *Vegetatio* 69: 169-175
- Nambiar, E.K.S. and Sands, R. 1993. Competition for water and nutrients in forests. *Canadian Journal of Forest Research*. 23: 1955-1968.
- Nelson, B.W. 1994. Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews* 10: 105-125.
- Niering, W.A. and Egler, F.E. 1955. A shrub community of *Viburnum lentago*, stable for twenty-five years. *Ecology* 36: 356-360.
- Niering, W.A. and Goodwin, R.H. 1974. Creation of relatively stable shrublands with herbicides: Arresting succession on rights-of-way and pastureland. *Ecology* 55: 784-795.
- Nilsen, E.T., Clinton, B.D., Lei, T.T., Miller, O.K., Semones, S.W., and Walker, J.F. 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? *American Midland Naturalist*. 145: 325-343.
- Nilsen, E.T., Walker, J.F., Miller, O.K., Semones, S.W., Lei, T.T., and Clinton, B.D. 1999. Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): Could allelopathy be a cause? *American Journal of Botany* 86: 1597 - 1605.

- Nilsson, M.C. 1994. Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. *Oecologia*. 98: 1-7.
- Nilsson, M.C., Zackrisson, O., Sterner, O., and Wallstedt, A. 2000. Characterisation of the differential interference effects of two boreal dwarf shrub species. *Oecologia*. 123: 122 - 128.
- Nolte, D.L. and Barnett, J.P. 2000. A repellent to reduce mouse damage to longleaf pine seed. *International Journal of Biodeterioration and Biodegradation* 45: 169 - 174.
- Nyland, R.D. 2002. *Silviculture: Concepts and Applications*. McGraw-Hill Higher Education, Burr Ridge, IL, U. S. A.
- Oliver, C.D. and Larson, B.C. 1996. *Forest stand dynamics: Update edition*. John Wiley & Sons, Inc., New York
- Orwig, D.A., Foster, D.R., and Mausel, D.L. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography* 29: 1475 - 1487.
- Ostfeld, R.S. and Canham, C.D. 1993. Effects of meadow vole population density on tree seedling survival in old fields. *Ecology* 74: 1792-1801
- Ostfeld, R.S., Manson, R.H., and Canham, C.D. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78: 1531 - 1542.
- Pacala, S.W. and Crawley, M.J. 1992. Herbivores and Plant Diversity. *American Naturalist* 140: 243 – 260.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs* 66:1 - 43.
- Pacala, S.W., Canham, C.D., Silander Jr., J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* 24: 2172 - 2183.
- Packer, A. and Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*. 404: 278 - 281.
- Palmer, S.C.F., Hester, A.J., Elston, D.A., Gordon I.J., and Hartley, S.E. 2003. The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. *Ecology* 84: 2877 - 2890.

- Payette, S. and Delwaide, A. 2003. Shift of conifer boreal forest to lichen-heath parkland caused by successive stand disturbances. *Ecosystems*. 6: 540 - 550.
- Perez-Salicrup, D.R. and Barker, M.G. 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124: 469-475.
- Peterson, C.J. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist* 124: 127-133.
- Peterson, C.J., and Pickett, S.T.A. 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. *Oikos* 90: 489 - 500.
- Petraitis, P.S. and Latham, R.E. 1999. The importance of scale in testing the origins of alternative community states. *Ecology* 80: 429-442.
- Pfitsch, W.A. and Smith, A.P. 1988. Growth and photosynthesis of *Aechmea magdalenae*, a terrestrial CAM plant in a tropical moist forest, Panama. *Journal of Tropical Ecology* 24: 199 - 207.
- Pianka, E.R. 1966. Latitudinal gradients in species diversity. *American Naturalist* 100: 33 – 46.
- Pizo, M.A. and Morellato, L.P.C. 2002. A new rain-operated seed dispersal mechanism in *Bertolonia mosenii* (Melastomataceae), a Neotropical rainforest herb. *American Journal of Botany* 89: 169-171.
- Porter, W. F. 1994. Burgeoning ungulate populations in national parks: is intervention warranted? Pages 304-312 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier, New York, New York, USA.
- Poulsen, A.D. and Balslev, H. 1991. Abundance and cover of ground herbs in an Amazonian rain forest. *Journal of Vegetation Science* 2: 315 – 322.
- Prescott, C.E., L.P. Coward, G.F. Weetman and S.P. Gessel. 1993. Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*) in two coastal Douglas-fir forests. *Forest Ecology and Management*. 61:45-60.
- Prévost, M. and Pothier, D. Partial cuts in a trembling aspen - conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Canadian Journal of Forest Research* 33: 1 - 15.
- Price, D. T.; Black, T. A.; Kelliher, F. M. 1986. Effects of salal understory removal on photosynthetic rate and stomatal conductance of young Douglas-fir trees. *Canadian Journal of Forest Research*. 16: 90-97.

- Proulx, M. and Mazumder, A. 1998. Grazer reversal of plant species richness under contrasting nutrient richness. *Ecology* 79: 2581-2592.
- Putz, F.E. 1991. Silvicultural effects of lianas. In *The biology of vines*. Cambridge University Press, New York, NY. pp. 493-501
- Putz, F.E. and Canham, C.D. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. *Forest Ecology and Management* 49: 267-275
- Quality Deer Management Association. 1999. White-tailed Deer Density Map 1999, [www.qdma.com](http://www.qdma.com) <<http://www.qdma.com>>.
- Raich, J.W. and Christensen, N.L. 1989. Malaysian Dipterocarp forest: Tree seedling and sapling species composition and small scale disturbance patterns. *National Geographic Research* 5: 348-363.
- Reader, J.J. 1997. Potential effects of granivores on old-field succession. *Canadian Journal of Botany* 75: 2224 - 2227.
- Reader, R.J. 1992. Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology* 73: 373 - 376.
- Reader, R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* 81: 169 - 175.
- Rees, M., Condit, R., Crawley, M., Pacala, S. and Tilman, D. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650-655.
- Reich, P.B., Grigal, D.F., Aber, J.D., and Gower, S.T. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78: 335-347
- Rey, P.J., Garrido, J.L., Alcantara, J.M., Ramirez, J.M., Aguilera, A., Garcia, L., Manzaneda, A.J., Fernandez, R. 2002. Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Functional Ecology* 16: 773 - 781.
- Rhoades, A.G. Hamburg, S.P., Fahey, T.J., Siccama, T.G., and Kobe, R. 2004. Comparing direct and indirect methods of assessing canopy structure in a northern hardwood forest. *Canadian Journal of Forest Research* 34: 584 - 591.
- Ricard, J.P., Messier, C., DeLaGrange, S., and Beaudet, M. 2003. Do understory sapling respond to both light and belowground competition?: a field experiment in a north-eastern American hardwood forest and a literature review. *Annals of Forest Science* 60: 749 - 756.

- Ristau, T.E. and Horsley, S.B. 1999. Pin cherry effects on Allegheny hardwood stand development. *Canadian Journal of Forest Research* 29: 73 - 84.
- Ritchie, M.E., Tilman, D. and Knops, J.M.H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79: 165-177.
- Robinson, J.G. and Redford, K.H. 1986. Body size diet and population density of Neotropical forest mammals. *American Naturalist* 128: 665-680.
- Rogers, R.S. 1981. Mature mesophytic hardwood forest: Community transitions, by layer, from east-central Minnesota to southeastern Michigan. *Ecology* 62: 1634-1647.
- Rogers, G.M. and Leathwick, J.R. 1997. Factors predisposing forests to canopy collapse in the Southern Ruahine Range, New Zealand. *Biological Conservation* 80: 325-338.
- Roldan, A.I. and Simonetti, J.A. 2001. Plant-mammal interactions in tropical Bolivian forests with different hunting pressures. *Conservation Biology* 15: 617-623.
- Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74: 201 - 208.
- Rooney, T.P. and Dress, W.J. 1997. Species loss over sixty-six years in the ground layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Natural Areas Journal* 17: 297-305.
- Rooney, T.P. and Waller, D.M. 2003. Direct and indirect effects of deer in forest ecosystems. *Forest Ecology and Management* 181: 165 - 176.
- Rooney, T.P., Wiegmann, S.M., Rogers, D.A., and Waller, D.M. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conservation Biology* 18: 787 - 798.
- Runkle, J.R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546 - 547.
- Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62: 1041-1051.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth forests of the eastern North America. *Ecology* 63: 1533-1546.
- Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Canadian Journal of Forest Research*. 20: 632-641.

- Russell, A.E., Raich, J.W., Vitousek, P.M. 1998. The ecology of the climbing fern *Dicranopteris linearis* on windward Mauna Loa, Hawaii. *Journal of Ecology*. 86: 765 - 779.
- Russell, F.L., Zippin, D.B., and Fowler, N.L. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist*. 146: 1 - 26.
- Sabhasri, S. and Ferrall, W.K. 1960. Invasion of brush species into small stand openings in the Douglas Fir forests of the Willamette Foothills. *Northwest Science*. 34: 77 - 88.
- Saunders, M.R. and Puettmann, K.J. 1999. Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine seedlings. *Canadian Journal of Forest Research* 29: 536 - 546.
- Schmitz, O.J. and Sinclair, A.R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. In *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC. pp. 201-223.
- Schnitzer, S.A. and Carson, W.P. 2000. Have we forgotten the forest because of the trees? *Trends in Ecology and Evolution* 15: 375-376.
- Schnitzer, S.A. Parren, M.P.E., and Bongers, F. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecology and Management* 190: 87 - 98.
- Schnitzer, S.A. and F. Bongers 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223-230.
- Schnitzer, S.A., Dalling, J.W., and Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*. 88: 655-666.
- Schnurr, J.L., Canham, C.D., Ostfeld, R.S., and Inouye, R.S. 2004. Neighborhood analyses of small mammal dynamics: Impacts on seed predation and seedling establishment. *Ecology*. 85: 741 - 755.
- Schnurr, J.L., Ostfeld, R.S., and Cahnah, C.D. 2002. Direct and indirect effects of mast on rodent populations and tree seed survival. *Oikos* 96: 402 - 410.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *American Naturalist* 122, 240-285.
- Schreiner, M., Bauer, E.M., Kollmann, J. 2000. Reducing predation of conifer seeds by clear-cutting *Rubus fruticosus* agg. In two montane forest stands. *Forest Ecology and Management*. 126: 281 - 290.

- Schupp, E.W., Howe, H.F., Augspurger, C.K. and Levey, D.J. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70: 562-564.
- Schurr, J.L., Cahnah, C.D., Ostfeld, R.S. and Inouye, R.S. 2004. Neighborhood analyses of small-mammal dynamics: Impacts on seed predation and seedling establishment. *Ecology* 85: 741 - 755.
- Seymour, R.S., White, A.S., and de Maynadier, P.G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management*. 155: 357 - 367.
- Shapiro, S.S. and Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591 – 611.
- Sharitz, R.R., Boring, L.R., Van Lear, D.H., and Pinder III, J.E. 1992. Integrating ecological concepts with natural resource management of southern forests. *Ecological Applications* 2: 226-237.
- Shugart, H.H. and West, D.C. 1977. Development of an Appalachian deciduous forest model and its application to assessment of the impact of the chestnut blight. *Journal of Environmental Management* 5: 161 - 179.
- Silman, M.R., Terborgh, J.W. and Kiltie, R.A. 2003. Population regulation of a dominant rain forest tree by a major seed predator. *Ecology* 84: 431 – 438.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16: 269 – 311.
- Sipe, T.W. and Bazzaz, F.A. 1995. Gap partitioning among Maples (*Acer*) in central New England: survival and growth. *Ecology* 76: 1587 - 1602.
- Smith, H. Clay. 1984. Forest management guidelines for controlling wild grapevines. Broomall, PA, USDA Forest Service, NE Experiment Station. Research Paper NE-548. 14 pgs.
- Smith, T.M. and Urban, D.L. 1988. Scale and resolution of forest structural pattern. *Vegetatio* 74: 143 - 150.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman Company, New York.
- Sork, V.L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68: 1341 – 1350.

- Steel, G. D., and J. H. Torrie. Principles and procedures of statistics, a biometrical approach. 2nd ed.. 1980. McGraw-Hill New York .
- Stiles, E.W. 2000. Animals as seed dispersers. In: Fenner M (ed). Seeds: the ecology of regeneration in plant communities. CABI, Wallingford, Oxon, United Kingdom, pp 111 – 124.
- Stoeckeler, J.H., Strothman, R.O., and Kreftint, L.W. 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *Journal of Wildlife Management* 21: 75 - 80.
- Stout, S.L. and Nyland, R.D. 1986. Role of species composition in a relative density measurement in Allegheny hardwoods. *Canadian Journal of Forest Research* 16: 574 - 579.
- Stromayer, K.A.K. and Warren, R.J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin* 25: 227-234.
- Suding, K.N., Gross, K.L., Houseman, G.R. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Systematics* 19: 46 – 53.
- Sun, S., Gao, X.M., and Chen, L.Z. 2004. High acorn predation prevents the regeneration of *Quercus liaotungensis* in the Dongling mountain region of north China. *Restoration Ecology* 12: 335 - 342.
- Sutherland, J.P. 1974. Multiple stable points in natural communities. *American Naturalist* 108: 859-873
- Sutherland, J.P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. *American Naturalist* 136: 270-275
- Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16: 284-307
- Tappeiner, J. C., II, J. C. Zasada, D. W. Huffman, and L. M. Ganio. 2001. Salmonberry and salal annual aerial stem production: the maintenance of shrub cover in forest stands. *Canadian Journal of Forest Research*. 31:1629 - 1638.
- Tappeiner, J.C. 1971. Invasion and development of beaked hazel in red pine stands in northern Minnesota. *Ecology*. 52: 514-519.
- Tappeiner, J.C. and John, H.H. 1973. Biomass and nutrient content of hazel undergrowth. *Ecology*. 54: 1342 - 1348.
- Tappeiner, J.C., Zasada, J., Ryan, P., and Newton, M. 1991. Salmonberry clonal and population structure: The basis for a persistent cover. *Ecology*. 72: 609 - 618.



- Taylor, A.H. and Zisheng, Q. 1988. Regeneration patterns in old-growth *Abies* and *Betula* forests in the Woolong Natural Preserve, Sichuan, China. *Journal of Ecology*. 76: 1204-1218.
- Taylor, A.H., Qin Zisheng and Liu Jie. 1995. Tree regeneration in an *Abies faxoniana* forest after bamboo dieback Wang Lang Natural Reserve, China. *Canadian Journal of Forest Research*. 25: 2034-2039.
- Terborgh, J., Lopez, L., Nunez, V.P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D. and Balbas, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923-1926.
- Terborgh, J. and Wright, S.J. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75: 1829-1833.
- Terborgh, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24: 283-292.
- Terwilliger, V.J. 1978. Natural history of Baird's Tapir on Barro Colorado Island, Panamá Canal Zone. *Biotropica* 10: 211 – 220.
- Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53: 524 - 532.
- Tobler, M.W. 2002. Habitat use and diet of Baird's tapirs (*Tapirus bairdii*) in a montane cloud forest of the Cordillera de Talamanca, Costa Rica. *Biotropica* 34: 468 – 474.
- Uhl, C., Clark, K., Dezzeo, N., and Maquirino, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751-763.
- Valladares, F., Wright, S.J., Lasso, E., Kitajima, K. and Pearcy, R.W. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81: 1925 – 1936.
- Vandermast, D.B. and Van Lear, D.H. 2002. Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecology and Management*. 155: 97-106.
- Veblen, T.T. 1982. Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bulletin of the Torrey Botanical Club*. 109: 474-487
- Von Ende, C.N. 2001. Repeated-measures analysis: Growth and other time-dependent measures. In Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Oxford University Press, NY, pp. 134-157.

- Wada, N. 1993. Dwarf bamboos affect the regeneration of zoochorous trees by providing habitats to acorn-feeding rodents. *Oecologia* 94: 403-407.
- Walker, J.F., Miller, O.K. Jr., Lei, T., Semones, S., Nilsen, E., and Clinton, B.D. 1999. Suppression of ectomycorrhizae on canopy tree seedlings in *Rhododendron maximum* L. (Ericaceae) thickets in the southern Appalachians. *Mycorrhiza* 9: 49-56.
- Walker, L.R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science*. 5: 525-532.
- Walker, L.R. and Boneta, W. 1995. Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. *Journal of Tropical Ecology* 11: 473 - 479.
- Waller, D.M. and Alverson, W.S. 1997. The white-tailed deer: A keystone herbivore. *Wildlife Society Bulletin* 25: 217-226.
- Walters, M.B. and Reich, P.B. 1996. Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77: 841 - 853
- Walters, R.S. and Yawney, H.W. 1990. *Acer rubrum* L. Red Maple. in *Silvics of North America, Volume 2, Hardwoods*. USDA Forest Service Agricultural Handbook.
- Wardle, D.A. and Nilsson, M.C. 1997. Microbe-plant competition, allelopathy, and arctic plants. *Oecologia* 109: 291-293.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., and Ghani, A. 2001. Introduced browsing mammals in New Zealand natural forests: Aboveground and belowground consequences. *Ecological Monographs* 71: 587-614.
- Wardle, D.A., Nilsson, M.-C., Gallet, C., and Zackrisson, O. 1998. An ecosystem-level perspective of allelopathy. *Biological Reviews* 73: 305-319.
- Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology*. 35: 1-22.
- Wayne, P.M., and Bazzaz, F.A. 1993. Birch seedling responses to daily time courses of light in experimental forest gaps and shadehouses. *Ecology* 74: 1500 - 1515.
- Webb, W.L., King, R.T., and Patric, E.F. 1956. Effect of white-tailed deer on a northern hardwood forest. *Journal of Forestry* 54: 391 - 398.
- Weidenhamer, J.D. 1996. Distinguishing resource competition and chemical interference: Overcoming the methodological impasse. *Agronomy Journal* 88: 866-875.
- Welandar J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. *Journal of Zoology (Lond)* 252: 263 – 271.

- Welden, C. W. and Slauson, W. L.. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology* 61: 23–44.
- Wendel, G.W. 1972. Longevity of black cherry seed in the forest floor. USDA Forest Service Research Note NE - 149, Northeastern Experimental Station, Upper Darby, PA, USA 4 p.
- Westoby, M., Walker, B.H., and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Rangeland Management* 42: 195 – 205.
- White, M.A. and Mladenoff, D.J. 1994. Old-growth forest landscape transitions from pre-European settlement to present. *Landscape Ecology* 9: 191 - 205.
- Whitmore, T.C., Peralta, R. and Brown, K. 1985. Total species count in a Costa Rican tropical rain forest. *Journal of Tropical Ecology* 1: 375 – 378.
- Whitney, G.G. 1990. The history and status of the hemlock-hardwood forests of the Allegheny Plateau. *Journal of Ecology* 78: 443 - 458.
- Williamson, G.B. 1990. Allelopathy, Koch's postulates and the neck riddle. In J.B. Grace and D. Tilman (eds.) *Perspectives on plant competition*. Academic Press, San Diego, CA. pp. 143-162.
- Willson, M.F. and Traveset, A. 2000. The ecology of seed dispersal. In Fenner M (ed). *Seeds: the ecology of regeneration in plant communities*. CABI, Wallingford, Oxon, United Kingdom, pp. 85 – 100.
- Wilson, D.E., Cole, F.R., Nichols, J.D., Rudren, R., Foster, M.S. 1996. *Measuring and monitoring biological diversity: standard methods for mammals*. Washington, DC. Smithsonian Institution Press.
- Wolff, J.O., Duesser, R.D., and Berry, K.S. 1985. Food habits of sympatric *Peromyscus leucopus* and *Peromyscus maniculatus*. *Journal of Mammalogy* 66: 795 - 798.
- Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut in the Great Smoky Mountains National Park. *Ecology*. 40: 349 - 361.
- Wright, S.J. 2002. Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia* 130: 1-14.
- Wright, S.J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. *Perspectives in Plant Ecology* 6: 73 - 86.
- Wright, S.J., Gomper, M.E., DeLeon, B. 1994. Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Islands. *Oikos* 71: 279-294.

- Wright, S.J., Zeballos, H., Dominguez, I., Gallardo, M.M., Moreno, M.C. and Ibanez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* 14: 227-239.
- Yamasaki, S.H., Fyles, J.W., Egger, K.N., and Titus, B.D. 1998. The effect of *Kalmia angustifolia* on growth, nutrition, and ectomycorrhizal symbiont community of black spruce. *Forest Ecology and Management*. 105: 197-207.
- Young, T.P., Chase, J.M., Huddleston, R.T. 2001. Community succession and assembly: comparing, contrasting, and combining paradigms in the context of ecological restoration. *Ecological Restoration* 19: 5 – 18.
- Youngblood, R. and Titus, B. 1996. Clear-cutting: a regeneration method in the boreal forest. *Forestry Chronicles*. 72: 31-36.
- Zackrisson, O., Nilsson, M.C., Dahlberg, A., and Jaderlund, A. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. *Oikos* 78: 209-220.